

The Development of Sociobiology in Relation to Animal Behavior Studies, 1946–1975

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Front page

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Abstract

This paper aims at bridging a gap between the history of American animal behavior studies and the history of sociobiology. In the post-war period, ecology, comparative psychology and ethology were all investigating animal societies, using different approaches ranging from fieldwork to laboratory studies. We argue that this disunity in "practices of place" (Kohler 2002) explains the attempts of dialogue between those three fields and early calls for unity through "sociobiology" by J. Paul Scott. In turn, tensions between the naturalist tradition and the rising reductionist approach in biology provide an original background for a history of Edward Wilson's own version of sociobiology, much beyond the William Hamilton's papers (1964) usually considered as its key antecedent. Naturalists were in a defensive position in the geography of the fields studying animal behavior, and in reaction were a driving force behind the various projects of synthesis called "sociobiology".

Introduction

In the immediate post-WWII period, animal social behavior was investigated by several overlapping scientific communities, at the frontier between biology and psychology. Ecologists, ethologists, and comparative psychologists represented distinct research traditions, ranging from naturalists to white-coat laboratory workers and blackboard mathematicians – leading to widely divergent representations of how "social" behavior in animals was to be accounted for.

Working in very different settings, both indoor and outdoor, these students of animal behavior interacted via key individuals and episodic debates, alternating between conflicting attitudes and calls to reach a synthesis. Against this background, Edward O. Wilson's sociobiology, while similarly devoted to "the systematic study of the biological basis of all social behavior" (Wilson 1975, 4), is

often conceived by the historiography as a relatively separate and later development. The goal of this paper is to flesh out the relation between sociobiology and the contemporary established fields studying animal social behavior in post-WWII America.

The result is a narrative where the history of sociobiology is woven with the history of ecology, ethology and comparative psychology. We identify the naturalists (and their concerns about animal behavior studies performed in the field) as a driving force in what became the sociobiological synthesis. Shifting attention to the various issues the naturalists' debates animated provides a richer understanding not just of sociobiology's formation but also of animal social behavior and of the subsequent history of post-1950s biology.

An attempt to write the history of sociobiology is bound to be surrounded with ambiguity: is it to be the history of a field, a term, or even a book? Some reviewers of Wilson's *Sociobiology: The New Synthesis* (Wilson 1975) suggested that the title of the book accomplished a performative act. Because it was a new label, with a definition attached to it, and a 697-page book embodying its principles, a new field called "sociobiology" would have thence been created in 1975 [1: "Then one day here rose up a man from among natural historians. He had been called Entomologist, Ecologist, and even Biochemist. But that was not enough. All grew quiet as he raised his golden pen: 'There shall be a new science,' he said, 'and it shall be called SOCIOBIOLOGY'" (West Eberhard 1976, 89). "A subject called sociobiology exists by virtue of the Cartesian syllogism, 'I have a textbook written about me, therefore I am a discipline.'" (Samuelson 1975). "A biochemist recently asked me to define sociobiology. The only simple answer to the question was 'The branch of biology covered in E.O. Wilson's book.'" (Krebs 1976, 709).]. Alternatively, one could consider that sociobiology, being defined by Wilson as the investigation of the biological origins of social behavior, was a subject with a history at least as old as Darwin's *Descent of Man* (1871) – rendering the history of so large a topic very diluted, and the origins of the label "sociobiology" relatively unimportant [2: "Wilson wrote the first modern synthesis of the accumulated literature on behavioral ecology and its related "skin-out" fields, especially ecology and evolutionary theory, and he promulgated the label "sociobiology," but that doesn't make him the field's father/founder. Who was? Darwin." (Stuart Altmann, email to the author, March 3, 2004).]. One could still choose to see sociobiology as mere *réchauffé* of late nineteenth, early twentieth century "social Darwinism," because of its potential or actual conservative implications (Cherry 1980; Lerner 1992).

However, most usually concur with Ullica Segerstrale's sociological account of the sociobiology debate, which considers that the "deep background" of sociobiology lays in the mid-1960s with William Hamilton's and Robert Trivers's articles on the evolution of altruism (Hamilton 1964; Trivers 1971; Trivers 1974) – a narrative at odds with Wilson's own view. [3: On the "deep background" of sociobiology, see (Segerstrale 2000, 79–99). In chapters both entitled "What is sociobiology?", (Kitcher 1985) and (Alcock 2001) take a similar view. Wilson flatly denies this historical reading of his work: "I was inspired to write *Sociobiology* not by the impetus of gene-centered theory of altruism as begun by Williams and Hamilton (and Haldane deserves some credit) although I admired the idea greatly and was pleased to include their work in a 1965 article on social insects and then in *The Insect Societies* in 1971." (Wilson, email to the author, April 16, 2009). This historical claim by Wilson should be put in the perspective of his recent reconsideration of the role of kin selection in the origins of eusociality (Nowak et al. 2010; Gibson 2012).]

These narratives leave a rich trove of materials unaddressed, worth incorporating in a history of sociobiology: the development through the 1950s and beyond of several disciplines claiming an interest in the biological study of the social behavior of animals, paving the way to initiatives

named “sociobiology”, well before Wilson’s use of the term. To the point, we claim that post-WWII animal social behavioral studies (ethology, comparative psychology and the Chicago school of ecology) were in a state of protracted conflict over their different traditions of indoor and outdoor studies. Wilson’s sociobiology, we will argue, can be profitably reconsidered as one of a series of attempts to resolve those tensions by defending the naturalist tradition in animal studies.

Recent works examining the field-laboratory border in twentieth century biology have emphasized the role of localization in the shaping of biologists’ practices, leading to very different styles of research and career paths depending on whether they worked in the field, a zoo, a museum or in the laboratory (Livingstone 1995; Weidman 1996; Finnegan 2008; Lightman 2016, 179–328). [4: Our framework bears an obvious debt to (Kohler 2002), which traces the history of American (mainly plant) ecology in this perspective, up to 1950. See also (Montgomery 2005) for a focus on primatologist C.R. Carpenter in the first part of the twentieth century, paying the same attention to scientific practice in situ; (Rees 2006) on the practices of the field of post-1950 primatologists, (Burkhardt 1999) for a brief history of ethology focusing on the problem of place, and (Billick and Price 2010) on ecology and place.] Typically, since the late nineteenth century, field biologists struggled to retain a sense of legitimacy at a time when standards of quantification and control elevated the laboratory and experimental science as the imagined future of biology (Benson 1991). Naturalists adapted techniques from the laboratory to the use in the field, developed their own tools, and invented protocols to reinvent the field as a place where “nature experiments” could be performed. These activities which necessitated new capabilities, such as field stations, transformed the traditional, observational natural history into “professional” ecology in the early decades of the twentieth century (Billick and Price 2010; Kingsland 2010). We argue that these tensions continued to play a role in post-1950 biology, and even heightened due to the coming of age of yet another mode of production of knowledge in contemporary biology, namely blackboard mathematical biology.

We will first depict the three main traditions of investigation of animal societies (ecology, comparative psychology and ethology), examining how they were situated at different places in the geography of scientific practices in mid-twentieth century, leading to divergent and equally problematic conceptions of the nature of “social” behaviors, and the methods to study them. We will then make the argument that this lack of unifying framework led outdoor biologists, who in this geography suffered from a recurring deficit of scientific credibility, to seek closer relations with experimental biology in order to develop an alliance, that behavioral geneticist J. Paul Scott called “sociobiology”. Once established that Scott’s sociobiology first emerged in the 1950s as a synthesis of laboratory and field based practices, it will be recognized that a similar pattern explains the forging of alliances by naturalists with mathematicians and theoretically minded biologists in the 1960s, resulting this time in Stuart Altmann’s and then Wilson’s sociobiology. This will lead us to reconsider in a last section the meaning of Sociobiology: The New Synthesis, and to suggest that this project led to reaffirming the naturalist credo in biology.

Troubles on the Lab-Field Border

Until the 1950s, ecologists at the University of Chicago were among the most visible students of social behavior in animals (Mitman 1992). [5: A mathematical approach to animal social behavior was developed at the same time by the “Committee of Mathematical Biology” of Nicolas Rashevsky in the same university. Lacking an adjunct empirical research program, it failed to gain much

traction among students of animal behavior (Abraham 2004; Shmailov 2016).] Drawing on a tradition of attention to the relationships between the organisms and their environment, students of animal behavior at the Department of Zoology emphasized the social relations in animal communities. The physiological gradients conceptualized by Charles M. Child, Ralph Gerard's notion of "orgs" encompassing both living beings and societies, Alfred Emerson's attachment to the concept of superorganism, and Warder C. Allee's stress on the adaptive role of cooperation in evolution were as many ways to think of animals not as a homogeneous collection of isolated individuals, but as integrated groupings (Mitman 1992). [6: Even Sewall Wright, who as a geneticist could have ignored the role of higher level interactions, stands out for suggesting a first analytical model of group selection – which buttressed his colleagues' efforts at Chicago to show that pro-social behavior was a force of evolution. (Wright 1945).] According to the definition of the "social" held at Chicago, the behavior of individual animals was to be explained as part of a subsuming whole functioning like a coherent system or organ, displaying physiological properties (Burns 1980; Banks 1985; Mitman 1992).

Interestingly, those integrated groupings were given different names and treatments, depending on the "practices of places" (Kohler 2002) used to investigate them. Social groups in nature were "communities", while they were "populations" when studied in the labs, or in the field but with standards of quantitative rigor meeting those of the lab (Allee et al. 1949, 265). The problem at Chicago was that they tended to attach as much if not more importance to the field as to the laboratory, at a time when funding was re-orientated towards a physics-inspired biology, designating clearly the laboratory as the preferred place to conduct science. [7: Once appointed Head of the Division for Natural Science at the Rockefeller Foundation, Warren Weaver promoted a "New Biology", also dubbed "experimental biology", which eroded the funding available to field biology (Kohler 1976, 286–287). "Molecular biology" was coined by officers of the Rockefeller Foundation in their Annual Report for 1938 (Abir-Am 1987, 32–33).] Indeed, Emerson, Allee and their colleague Karl Schmidt were especially keen on field work: "seasoned tropical biologists", they all "shared a certain fondness for life in the jungle." (Mitman 1992, 103) Allee lamented that he "want[ed] students with a love for field work which even the handicap of living in the city of Chicago cannot quench." "I am tired of working with man-made, degree-hunting graduate students in zoology. I welcome the natural naturalist who cannot be kept out of field work even though his doctor's or other research lies elsewhere." (Allee 1930, 630).

This attitude also translated into the debates on the levels of selection in evolutionary theory. Some among the younger generation of students reacted negatively to the "good of the species" brand of argument which was commonplace among naturalists. Based on statistical analyses of homogeneous populations in labs, rather than in the field, the renunciation to its fitness by the individual for the benefit of a community was judged a logical impossibility. "If it was biology Emerson was discussing, I would be better off selling insurance," recalls evolutionary biologist George Williams about his attendance to a conference at Chicago in 1957 (Brockman 1995, 40). In sum, Chicago ecologists were situated right on the border between the field and the laboratory, which put them in an unstable position. While they studied populations in the laboratory as a complement to the investigation of natural communities in the field, the new biology used the laboratory to cancel the noise of social interactions and isolate the evolutionary destiny of homogeneous, asocial populations.

In contrast, the immense majority of comparative psychologists conducted their science indoor, which spared them the legitimacy issues faced by field ecologists. But their definition of "social

behavior” turned out to be equally problematic, though in a different way. Whereas ecologists at Chicago worked in the field and in the laboratory, the privileged techniques and location of comparative psychology were quasi-exclusively those of the laboratory, affording a tight control of environmental parameters and precise measurements. This rigor was contrasted with the perceived unscientific, subjectivist methods of field biologists, whose outdoor activities could allow neither the full description nor the reproducibility of observations.

Most contributions in comparative psychology reported experiences of individual animals engaged in exercises of maze-learning or sensory discrimination under various stressful conditions. Individual behavior was understood as a manifestation of the subject’s inner physiological drives, susceptible of modification through physiological manipulations and conditioning (via reinforcement or punishment). In the relatively rare instances when social behavior was under scrutiny, comparative psychologists proceeded by replicating their methodological approach to the study of single animals. [8: In the early days of comparative psychology, the investigation of social behavior was included in the agenda the discipline traced for itself (Holmes 1922). The clarification that “minding” (we would say “cognition” today) had always been the actual matter of interest, rather than “behavior” in full, is stated in a rare defense of the classic program of comparative psychology by William Mason (Mason 1980). On average, between 1921 and 1974 less than 10% of the articles published in the *Journal of Comparative Psychology* were concerned with social behavior. For similar bibliometric surveys, see (Schneirla 1946; Beach 1950; Lown 1975).] This approach to social behavior, by comparing the “normal” social trait with highly perturbed states, was conducive to a peculiar understanding of sociality and behavior. Indeed, comparative psychologists regularly expressed their wish for sounder theoretical motivations to their scientific enterprise, looking at ethology alternatively as a potential inspiration for reform, and as a threatening competitor. [9: The often-cited example of absurd confusion between natural and artificial settings is the mention by a comparative psychologist of the “natural cage conditions” (emphasis added (Burkhardt 1999, 500). A list of calls to reform comparative psychology by insiders includes (Schneirla 1946; Beach 1950; Hodos and Campbell 1969; Chiszar 1972).]

In comparison with the experimental approach to the study of social behavior privileged by comparative psychologists, the defining feature of ethologists has sometimes been said to be that they loved the animals they studied (Dewsbury 1992, 209; Burkhardt 2005, 312). Ethology achieved international scientific standing in the post-war period with the works of Dutch Niko Tinbergen and Austrians Karl von Frisch and Konrad Lorenz. Contrary to comparative psychologists, ethologists did not try to identify the physiological origins of social behavior with laboratory experiments, followed by dissections and physiological analyses. Instead, they claimed the merits of considering a rich variety of species and the importance of spending long hours at animal watching, so as to surely identify the original, “untouched” behaving of animals. Focused on the full range of behavior rather than on the functioning of high level cognitive abilities, ethologists downplayed the importance of learning and insisted on the instinctual, innate patterns of behavior. [10: On the ethology and comparative psychology traditions and the parallel divide between naturalist and laboratory traditions, see (Jaynes 1969). To Jaynes, the gist of the difference is that naturalists study animals “not as corpses reeking with formaldehyde in the Cuvierian tradition, but as living things in their habitat.” (on p. 602).]

Natural or semi-natural settings obviously allowed for an increased attention to social behavior. In open fields and with free movements, phenomena like imprinting, gregariousness, mating, conflict or cooperation were more readily observed than by confining single animals in mazes or Skinner

boxes. [11: Comparative psychology did develop “open-field” experiments in the 1960s, but it featured individual animals raised in captivity, for which the “open field” (a measured, artificial perimeter) appeared as an unusual and frightening experience (e.g., Candland and Campbell 1962).] Yet, the import of ethology in the United States did not go without concerns for its scientific credentials. Comparative psychologists were quick to point to their relative strength in quantitative methods, and to dismiss the ethologists’ too strong insistence on the innate nature of animal behavior, to the detriment of an attention to the development and learning stages, necessary for the individuals to acquire their full pattern of behavior. [12: This different appraisal of the instinctive nature of social behavior reflected the established consensus in the post-war American society that “culture” was irreducible to biological explanations – to argue the contrary was risking being accused of social Darwinism (Bellomy 1984). In this respect, social behavior in animals occupied an ambiguous position: was it as strongly determined by Darwinian evolution as physical characters were, or did it belong to a different order of phenomena entirely, as in an embryo of culture? Behaviorists and comparative psychologists considered that environmental factors played a larger role, and were suspicious of the determinism implied by the evolutionary view. These divergent views were made fully apparent in the criticism of Lorenz’ ethology by comparative psychologist Daniel Lehrman (Lehrman 1953; Burkhardt 2005, 384-390).]

This categorization of animal behavior studies circa 1950 in three currents (ecology, ethology, comparative psychology) has sometimes being criticized for its arbitrariness, since a number of individuals tried to render them interfecund, leading to exchanges of concepts, techniques, and to common publications (Dewsbury 1992). Some comparative psychologists did conduct field studies, and some ethologists had a preference for observations in semi-natural conditions, rather than in the complete wilderness. [13: As Burkhardt notes, Lorenz studied semi-domesticated animals in the enclosed fields adjacent to his father’s large house in Altenberg, Austria. Zoos were other privileged artificial settings frequented by naturalists (Mitman 1996; Burkhardt 1999; Burkhardt 2005).] We contend here that distinguishing the features of these fields, while acknowledging the influences and overlap between them, does not impede our comprehension of animal social behavior studies at the time. To the contrary, identifying the tensions between these fields, in particular the long standing competition for scientific credibility between naturalist and laboratory-based traditions, is key to the understanding of the recurrent calls to synthesis in animal behavior studies in the 1950s and beyond. Often presented as idiosyncratic projects (as in “Wilson’s sociobiology”), we want to represent them now as responses to a common need: building up legitimacy by making alliances between the laboratory and field research traditions.

The Committee for the Study of Animal Societies under Natural Conditions

The first use of the term “sociobiology” in the post-war period nicely illustrates the attempts for the three traditional fields investigating the social behavior of animals to communicate on a common platform. In 1946, a conference sponsored by the Rockefeller Foundation was convened at the Jackson Memorial Laboratory, Bar Harbor, Maine, under the supervision of behavioral geneticist J. Paul Scott (Paul 1998). Scott had the profile to be a go-between for the three fields. A former student of Allee and Wright at Chicago, he had demonstrated an interest both for field and laboratory studies. Working on organisms ranging from fruit flies to mammals, and director of behavioral studies in the national center for the production of laboratory rats, he was well-prepared to act as a

synthesizer of various approaches to animal behavior studies. Indeed, if the conference on “Genetics and Social Behavior” was supposed to launch a Rockefeller project to demonstrate the genetic basis of intelligence, Scott and the participants “hijacked” the conference and made it deliver an unexpected outcome (Scott 1985; Scott 1989). [14: Founded in 1929 by C. C. Little to study the heredity of cancer, the Jackson Laboratory had become one of the main suppliers of inbred mice for cancer research in the United States. It remains an important center in mammalian genetics to this day (Mitman 1992; Paul 1998; Rader 2004).]

The audience gathered a sample of scientists from ecology and comparative psychology, sympathetic to a dialogue of their fields with ethology. Hence, the comparative psychologists in attendance were notable for having expressed an unusual interest in the study of animal behavior under natural conditions, rather than in their familiar laboratories. Robert Yerkes, who chaired the conference, was the towering figure of comparative psychology, and came from a time when the discipline used many more animal models, in a variety of settings. [15: Yerkes had founded in 1911 the *Journal of Animal Behavior*, first American journal devoted to the study of the topic. The journal was discontinued in 1917, to reappear in 1921 as the *Journal of Comparative Psychology*.] C. R. Carpenter, a former fellow of Yerkes’s “monkey farm”, was also among the audience. He was praised by Scott who had an enormous respect for his work on the howling monkeys, stressing that it was “the first major study of mammalian society under natural conditions.” (Carpenter 1934; Scott 1985, 414). The audience also comprised two other figures in comparative psychology, both in the forefront of the criticism of the overwhelming position of laboratory studies in their field. Frank Beach, Curator of the Department of Animal Behavior at the American Museum of Natural History until this year, was receptive to Tinbergen’s ethological approach to animal behavior studies, and would address a scathing criticism of comparative psychology as performed by its flagship journal, that he suggested should be renamed “The Journal of Rat Learning” (see Figure 1) [16: In 1947, Beach met with Tinbergen who was visiting the United States. The six-lecture series given by Tinbergen at the American Museum and Columbia University would constitute the material for *The Study of Instinct*, published in 1951 (Burkhardt 2005, 292, 362-366).].

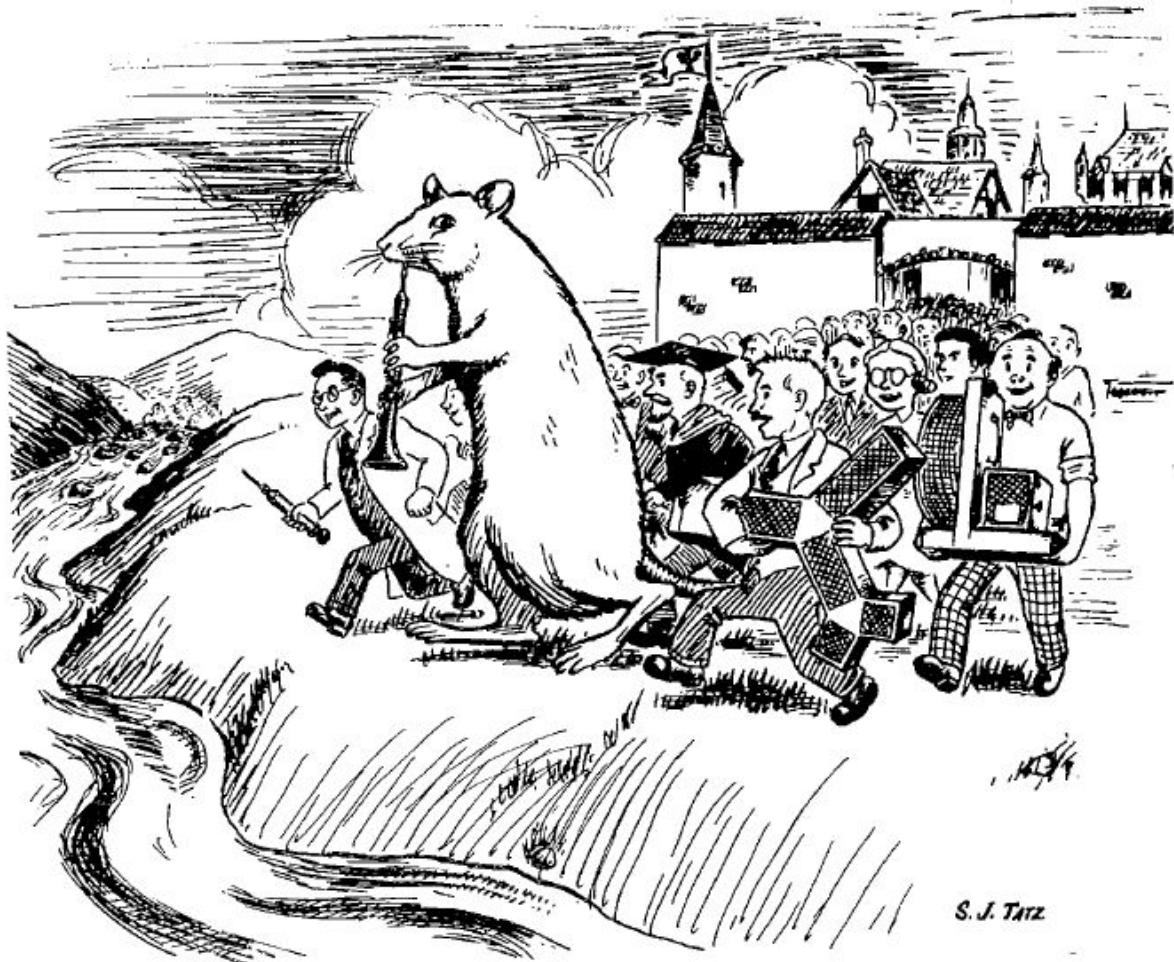


FIG. 3. Current position of many experimental psychologists.

Figure 1. The fate of comparative psychology, envisioned by Beach. Note the T-maze and the running wheel. From Beach (1950, 118). Reproduced with permission

T.C. Schneirla was the other prominent comparative psychologist present at the conference with also a strong interest in field studies. Specializing in ants, he had co-authored a classic textbook in comparative psychology replete with studies of rat maze learning, but had also published an acclaimed study of army-ants, observed in the field in Barro Colorado Island in 1932 and 1936 (Schneirla 1933; Maier and Schneirla 1935; Schneirla 1938; Tobach 2000) [17: Barro Colorado Island, together with Cayo Santiago Island (see below in the text), have been major centers for the study of animal social behavior and for the socialization of the scientists involved in those studies. Allee spent three months on Barro Colorado in 1924, Emerson six months in 1935, and Schmidt some time circa 1930 (Schmidt to Schneirla, March 1, 1948, Schneirla Papers, Box M579, Folder “Business Support for Research”, Theodore C. Schneirla Papers, Archives of the History of American Psychology, The University of Akron, hereafter cited as “Schneirla Papers”).].

Reflecting the participants’ pluralistic approach to the study of social behavior, the Bar Harbor conference called for a conjoint development of field and laboratory studies. An outcome of the conference was the creation of a “Committee for the Study of Animal Societies under Natural Conditions” (CSASNC) to translate this goal into practice. By wedding the best practices of comparative psychologists to those of the naturalists, the result would be a synthesis “between the fields of biology (particularly ecology and physiology) and psychology and sociology.” “Many names have been given to it, but perhaps the best and most descriptive is ‘sociobiology’,” Scott indicated at the first conference organized by the CSASNC (Scott 1950, 1003–1004).

This blend of practices would need a suitable place to flourish, at mid-range between the laboratory and the complete wilderness. Island biological stations fitted these constraints. Straightforwardly, insularity meant that one of the great features of the laboratory, isolation, was reproduced in preserved natural settings – without the artificiality of man-made walls and cages. Precise census work could then be performed, opening the way to demographic measurements and controlled manipulations of the structure of social groups. Hence, the CSASNC urged that Barro Colorado Island should “be put on a permanent basis of support as a center of tropical research” (Scott 1947, 208). Islands would also play a crucial role in the genesis of Altmann’s and Wilson’s versions of sociobiology [18: Barro Colorado Island was formed by the flooding of a valley, at the creation of the Panama Canal. It was transformed into a natural reserve in 1923. It is then a perfect example of the man-made character of the “natural” places singled out by sociobiologists. On the convenience of islands for census work on ants, see Schneirla to Diamond, October 20, 1953, Box M585.2, Folder “Public relations”, Schneirla Papers.].

The CSASNC acted as a provider of resources for the informal network of naturalist minded students of animal social behavior. Through a typed newsletter sent regularly by Scott, CSASNC members and “correspondents” were told about available grants, places suitable for naturalistic study, and job openings [19: Six newsletters were issued between June 10, 1949 and November 1956: Box M579, Folder: “Committee for Study of Animal Behavior”, and in box M585, Folder “CSASUNC”, both in the Schneirla Papers. The newsletter (n.d.) including the minutes from the CSASNC meeting in New York December 29, 1949 lists 28 members (elected to the committee) and 56 correspondents (simply receiving the committee reports and news).]. The newsletters also performed an organizational function, several including a listing of members and correspondents, or serving as call for papers and programs for the yearly meetings of the CSASNC. Sub-committees were created to collect a bibliography on field instruments, or to encourage field trips to Barro Colorado Island. In 1948, the first conference of the CSASNC in New York led in 1950 to the publication of papers on the “Methodology and Techniques for the Study of Animal Societies,” edited by Scott. This collection provided the first elements of a synthesis between laboratory and field studies. Field workers showcased an updated toolbox for outdoor studies, demonstrating a conciliatory attitude towards laboratory studies [20: One attempt was particularly diplomatic, when ecologist John Calhoun suggested borrowing from comparative psychologist their expertise at controlling conditions, but also their favorite subject, the rat (Calhoun 1950). Calhoun would continue to situate his studies of rat crowding and sociopathy in increasingly controlled and symbolically charged environments (Ramsden and Adams 2009).]. In Scott’s perspective, sociobiology was to be the organizational vehicle through which naturalists could gain a renewed visibility for field work, at a time when they felt academic journals were becoming less open to this type of research:

All of this [the activities of the CSASNC], I think, will tend to work in the direction of both building up interest in animal behavior and sociobiology and thereby making it possible to do what we talked about at the [New York] conference, namely to organize a new journal for this type of work. In spite of the cordial attitude of the editors of various existing journals, my own experience and that of others who have worked in the field leads me to believe that it is often very difficult to fit papers to the individual requirements of these journals.

— JP Scott to TC Schneirla, Scott to Schneirla - July 9 1948 - Box M579 - Folder “Conferences: Behavior Committee” Schneirla papers.

Hence sociobiology, as it was first coined and developed by the CSASNC, arose as a form of appeasement to contemporary tensions between field and laboratory studies in animal social behavior studies. It was adamant that the naturalist tradition was an asset rather than a hindrance for the scientific study of animal behavior. The task for sociobiology was precisely to develop a rigorous approach to field studies in order to match the methodological rigor expected by biologists working in the laboratory. This striving for an alliance between naturalists and their colleagues working indoor was at the core of Scott’s sociobiology, as it would be in Altmann’s and Wilson’s.

Through the late 40’s and 50’s, the CSASNC adopted a more and more formal structure and it became a regular feature of the joint annual meetings organized by the Ecological Society of America (ESA) and the American Society for Zoology (ASZ) to sponsor a session on “Animal Behavior and Sociobiology.” In 1956, a “Section On Animal Behavior and Sociobiology” was eventually created within the ESA, and it gained more than 300 members in less than a year [21: See “Newsletter” by Scott, November 1956, Box M585, Folder “CSASNC”, Schneirla Papers. In 1958, the ASZ would also burgeon a “Division of Animal Behavior”. By 1964, members from this Division would join those of the Section On Animal Behavior and Sociobiology to create their own society devoted to the study of animal behavior: the Animal Behavior Society. See “The Animal Behavior Society: Its Early History and Activities”, Schein, May 1976, Box M3796, Folder “ABS: History and Origins”, J.P. Scott Papers, Archives of the History of American Psychology, The University of Akron. The society kept true to the naturalist ethos that had inspired the CSASNC: “It seemed most important that the society should never lose sight of its basic unifying theme that all really relevant research on animal behaviour must eventually be related to the natural conditions under which the behaviour has evolved. We therefore wrote into the constitution the statement that ‘The Editor of the Journal shall encourage balances publication of both field studies and laboratory studies having fundamental relationship to the natural life of animals.’ ” (Collias 1991, 627).]. It is at this point that the young Wilson established contact with this new current of animal social behavior studies, via his student Altmann.

Primateology on Cayo Santiago: Sociobiology, Redux

In Fall 1953, two years into his graduate studies at Harvard, Wilson had attended a conference by Tinbergen and Lorenz on an American tour, who were lecturing on the “new science of ethology”

(Wilson 1994, 285) [22: This series of conference has had a considerable impact not just on Wilson, but on the American public in general (Emlen 1996, 178; Burkhardt 2005, 370–407).]. Lorenz, the passionate naturalist and animal-lover, made a decisive impression on the similarly inclined Wilson:

Then Lorenz came ... He was a prophet of the dais, passionate, angry, and importunate. He hammered us with phrases soon to become famous in the behavioral sciences: imprinting, ritualization, aggressive drive, overflow; and the name of the animals: graylag goose, jackdaw, stickleback. He had come to proclaim a new approach to the study of behavior. Instinct had been reinstated, he said; the role of learning was grossly overestimated by B.F. Skinner and other behaviorists; we must now press in a new direction. He had my complete attention. Still young and very impressionable, I was quick to answer his call to arms. Lorenz was challenging the comparative psychology establishment. ... My thoughts now raced. Lorenz has returned animal behavior to natural history. My domain. Naturalists, not psychologists with their oversimple white rats and mazes, are the best persons to study animal behavior.

— Edward O. Wilson, *Naturalist* (1994) pp. 285–287 - italics in the original

Wilson was not aware that his feelings against “rats and mazes” comparative psychology and behaviorism, or his enthusiasm for naturalist studies, were particularly close to those of the CSASNC members [23: “Unfortunately, Wilson and I had very little contact prior to the publication of his 1975 volume. People kept telling me about a bright young man working with social insects. But entomologists are a breed apart from other biologists; the insect world is their universe, and Wilson never came to the Animal Behavior Society Meetings.” (Scott 1985, 405) This is not an entirely convincing explanation, as Schneirla and Emerson were entomologists and founding members of the CSASNC, and as Wilson was named a Fellow of the Animal Behavior Society in 1968.]. But he did not remain isolated for long. In 1955, Wilson had just finished his Ph.D. dissertation on the ant genus *Lasius* when the Harvard administration asked him to supervise a post-graduate student, one year younger than him.

This student, Stuart Altmann, had specialized in the study of social behavior of rhesus macaques, and had thereby developed strong connections with the primatologists involved in the CSASNC [24: In 1955, Altmann had done howler monkey census work in the biological station on Barro Colorado Island, where Schneirla had done his renowned field work in the 1930s and 1940s. This also put Altmann in touch with Carpenter, who had done the original census in Barro Colorado in 1932 and 1933. Collias, another founding member of the CSASNC, had also done census work on this population of howler monkeys in 1951. The early career of Altmann and his contacts with Carpenter are accounted in (Haraway 1981; Haraway 1983; Haraway 1989).]. Carpenter had given Altmann the census data of another colony of rhesus monkeys he had implanted himself in the late 1930s on Cayo Santiago Island, off the coasts of Puerto Rico. In the 1940s, the biological station of Cayo Santiago had suffered a lack of funds, interrupting census work while the population of monkeys was decimated by shortage of food and removals for civil and war-related research

(Rawlins and Kessler 1986, 29). In 1956, behavioral research on social primates resumed with Altmann traveling to Cayo Santiago, his doctoral supervisor Wilson accompanying him:

My interest in sociobiology was not the product of a revolutionary's dream. It began innocently as a specialized zoology project one January morning in 1956 when I visited Cayo Santiago, a small island off the east coast of Puerto Rico, to look at monkeys. ... The two days Stuart [Altmann] and I lived among the rhesus monkeys of Cayo Santiago were a stunning revelation and an intellectual turning point ... In the evenings Altmann talked primates and I talked ants, and we came to muse over the possibility of a synthesis of all the available information on social animals. A general theory, we agreed, might take form under the name of sociobiology [26: Altmann: "The term 'sociobiology' was, for me, a natural extension of the term "psychobiology," which Robert M. Yerkes, in the Yale Psychology Department, had coined, to indicate a (hoped for) rapprochement between the two fields. Scott used the term four times in his 1950 Foreword to the publication (*Annals NY Acad Sci.*, 51(6)) of the results of a conference on "Methods and techniques for the study of animal societies." Perhaps it was also used in chapters in that conference proceedings. The volume is logged as number 135 in my collection, and so was one of the first reprints that I owned, and I am fairly sure that I had a copy with me during my two years on Cayo Santiago. Whether I got the term from there or from the obvious extension of Yerkes' term, I cannot say." "I was, in one sense, the first sociobiologist, in that, at my request, I was hired as a sociobiologist when I went to work at the Yerkes Regional Primate Research Center, in 1965. So far as I know, no one else had such a job title at that time." (Altmann, email to the author, March 3, 2004).].

— Edward O. Wilson, *Naturalist* (1994) pp. 308-310

The naturalist approach was still at the heart of this envisioned sociobiology, as Altmann's starting point was the collection over two years of ethograms and measurement of frequencies of behavioral displays in the wildlife of Cayo Santiago. However, as in Scott's case, what would be constitutive of sociobiology was the wedding of typical naturalist practices with those from "indoor" biology, as a means to overcome the deficit of credibility of traditional naturalist studies. Hence, Altmann did not rely on the notion of "releaser" as he did for the concept of ethogram, considering that it would introduce "gratuitous" assumptions on the sequential orders of behavioral patterns (Altmann 1965). He would have them better ascertained from scratch by a sociometric analysis, demanding skills borrowed from statistics [27: The choice of Cayo Santiago for the place where to conduct the sociobiology of primates was also revealing of the delicate balance to be struck between field and other (lab) practices, as readily acknowledged by the scientific workers on the island. "Cayo Santiago frees investigators from restrictions imposed by problems in the field which limit long-term observations on groups of wild animals, and which often result in a

superficial view of the complex behavioral interactions that comprise and sustain social network. ... Cayo Santiago offers an effective compromise between laboratory and field conditions because its free-ranging animals live relatively undisturbed in a seminatural habitat and are easily seen.” (Rawlins and Kessler 1986, 13). Similarly, Barro Colorado Island was often presented as a hybrid of “jungle” and “laboratory”, especially when addressing to a lay audience (Allee and Allee 1925; Coursen 1956). This hybrid nature was periodically renegotiated, as when tracts of forest were cut down to make place for a new laboratory building (see Catharine Reed to Schneirla, June 8, 1956; Schneirla to Reed, June 22, 1956, Box M585.1, Folder “Barro Colorado I”, Schneirla Papers).].

On top of the blending of different methodological traditions to collect and establish the empirical validity of field observations, Altmann and Wilson considered that an improved theoretical framework was necessary to extend the lessons from this case study of a single animal society to a comparative study of all social behaviors in animals. Altmann’s own preference was with a cybernetic approach to communication. Looking for an elementary language able to univocally describe the wealth of social networks existing across species, he came to the view that the theory of information and communication, as developed by Norbert Wiener, was such a tool (Altmann 1962; Altmann 1965; Altmann 1967; Haraway 1981) [28: CSASNC’ sociobiologists could accommodate with Altmann’s framework, as when John Emlen (ornithologist, participant in the 1946 Barr Harbor conference) adopted the language of control and communication to describe a “program of study into the general sociobiological mechanisms of cultural diffusion and maintenance in primate social groups.” (Gordon Stephenson and John Emlen, circa 1971, cited in (Haraway 1983, 188).].

This signaled an important shift in animal behavior studies, with the field and the laboratory being now supplemented by an additional legitimate place of production of knowledge: the blackboard. Conclusions derived from the development of mathematical models, traced on a blackboard by a researcher with possibly no prior training in zoology – and more probably in physics or engineering, would gain greater and greater credit, in a remarkable and rapid shift from the situation of the last years (Keller 2002, 79–89). At first, Wilson followed a route similar to Altmann’s, relying on the concept of feedback loops and the formalism of information theory when analyzing mass-foraging in ant societies (Wilson 1963; Haraway 1981). But the competitive environment at the Department of Biology at Harvard seems to have pushed Wilson to find a more definitely authoritative tool to achieve a unified theory of animal social behavior.

The Sociobiologist as a “Mathematician Naturalist”

Since the 1930s, institutional and financial resources for biological science had been increasingly redirected away from natural studies, to fund what would be called “molecular biology”. Warren Weaver, head of the Natural Science Division within the Rockefeller Division, was instrumental in imposing the vision that biology should get its inspiration from physical sciences. In his view, “ecology was glorified natural history.” (Mitman 1992, 105) [29: On Weaver, the Rockefeller Foundation and the development of molecular biology, see (Kohler 1976; Abir-Am 1982; Kohler 1991; Kay 1996).]. This stance, and the incontestable results achieved by molecular biologists, seriously threatened the future of animal studies in biology departments [30: On the conflict between the naturalist tradition and the rising molecular biology, see (Hagen 1999) in systematics, (Johnson 2008) in zoology, and (Dietrich 1998) in evolutionary biology. Of course molecular biology

is a laboratory and experimental science, but it draws on physics, chemistry and mathematics in a way that traditional experimental biology (e.g., morphology) never did. See Haraway (1989, 394–395) for a similar account of Wilson’s rivalry with Watson and the role it played in the sociobiology project.].

The atmosphere of these days at Harvard is nicely crystallized in an oft-quoted anecdote told by Wilson about the Department of Biology, which also hosted James Watson, co-discoverer of the structure of the DNA in 1953:

One day at a department meeting I naively chose to argue that the department needed more young evolutionary biologists, for balance. At least we should double the number from one (me) to two ... I proposed, following standard departmental procedure, that [a specialist in environmental biology] be offered joined membership in the Department of Biology. Watson said softly, ‘Are they out of their minds?’ ‘What do you mean?’ I was genuinely puzzled. ‘Anyone who would hire an ecologist is out of his mind,’ responded the avatar of molecular biology.

— Edward O. Wilson, *Naturalist* (1994) pp. 219–220

Molecular biology had renewed the faith in reductionism, and made animal behaviorists studying whole organisms in the field look simply wrong headed. Complex social forms would be deciphered by looking at their putative genetic basis, which implied skills in physical chemistry (and the mathematical foundations it supposed) that most naturalists lacked. Wilson himself did not feel at ease with mathematics but was eager to catch up, sensing that in these “molecular wars”, naturalist studies could be saved by (and had no choice but) strengthening their scientific status by drawing on the prestige of some mathematical biology. As he puts it, the alternative was to be relegated in museums and looked down as mere “stamp collectors.”

After his encounter with Altmann and his reaction against behaviorism, this was another strong motive to work at a synthesis, aiming at preserving the naturalists’ credo and upgrading it to the required scientific standards of the day. Sociobiology would be the comparative study of the biological roots of social behavior where the wide knowledge of species and observation skills of the naturalists would be an asset, and a unifying theory of social behavior formulated in advanced mathematics expressions – providing an authoritative analytical framework on par with the scientific status of molecular biology.

The time was ripe for such an alliance between naturalists and mathematicians. Since the early twentieth century, population ecology had developed into a mathematical science. Inspired by the successes of differential calculus in physics and chemistry, mathematical formalisms had slowly been imported in biology to study problems in demography, epidemiology, and ecology (Kingsland 1995). Alfred Lotka (1880-1947) was an early promoter of this approach, and if he failed to reach true recognition outside demography in his lifetime, his work inspired many natural and social scientists in the post-war period.

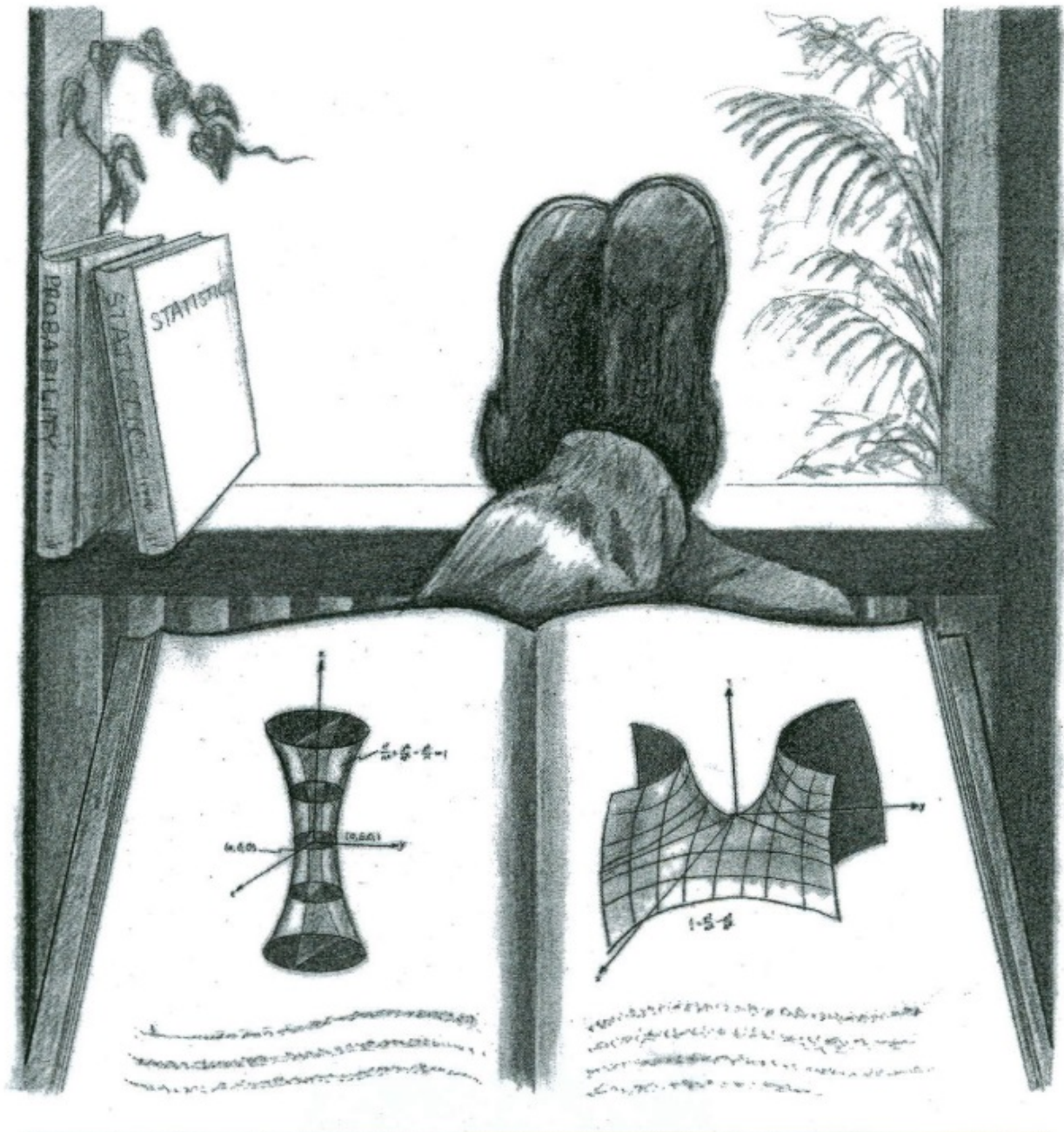


Figure 2. Wilson pictured working on his mathematics in 1961, symbolically and literally hanging on the border between indoor and outdoor biology. From Wilson (1994, 243)

One of them was ecologist G. E. Hutchinson, whose student Robert MacArthur became a collaborator of Wilson [31: Wilson and MacArthur belonged to a larger informal group of biologists and mathematicians interested in the mathematization of natural science, comprising Richard Lewontin, Richard Levins, and Egbert Leigh.]:

Although [MacArthur] had majored in mathematics at Marlboro College, and had a conspicuous talent for it, his heart was in the study of birds. He was a naturalist by calling, and seemed happiest when searching for patterns discovered directly in Nature with the aid of binoculars and field guides. ... As a mathematician-naturalist he was unique [...].

— Edward O. Wilson, *Naturalist* (1994) pp. 244 - our italics.

Hence in Wilson's memory, what MacArthur chiefly brought to their collaboration was the ability to think about ecological problems as a physicist or mathematician, while retaining at heart an identity of a naturalist. This fitted perfectly Wilson's agenda: to bring the physicist' mechanist metaphor and mathematical sophistication to the rescue of naturalist studies.

However, models in population ecology focused on interspecies relationships, and remained silent on the more essential forms of social behavior observable at a lower, intra-species level. To account for the latter, Wilson followed a similar strategy: he relied on recent developments in mathematical modeling by the British naturalist William Hamilton (Segerstrale 2013), whose mathematical analysis of altruism in social insects had come to his attention. Hamilton provided a simple rule which reinterpreted diverse forms of social behavior among kin as the outcome of a cost-benefit Darwinian calculation at the gene level, with the benefits brought to inclusive fitness outweighing the costs to individual fitness borne by the performer of the altruistic act. This rule was presented using a maximization principle and sophisticated mathematical formalizations not typical of a naturalist' training. It epitomized the values of abstract reasoning and generalization by the enunciation of laws in the tradition of mathematico-physics becoming ever more present in contemporary biology.

Thence, Hamilton's rule helped reintroduce social behavior in the series of topics studied by modern biology. This gene-centered view of sociality also replaced the "survival of the species" brand of argument that had made Williams gasp. Naturalists had found a new legitimacy in concentrating their efforts on social groupings; they had reintegrated the orthodox Darwinian framework.

It is not often stressed that in addition to the presentation of his mathematical model, Hamilton's papers contained a lengthy and technical discussion of its relevance for many instances of social species, supported by a wealth of observational studies (Hamilton 1964). The social aspects of behavior being most easily studied in the field, this comforted the naturalists in the position of main providers of the empirical material supporting mathematical models of sociality, and (especially if they agreed to train in math) as the most able to extend these models to a variety of situations. Indeed, beyond the presentation of elementary principles in theoretical population biology in its first chapters, Sociobiology provided an empirical validation of these principles by illustrating them with an encyclopedic survey of observational studies of social species [32: The visuals of the book bring testimony of the importance of the naturalist tradition in Wilson's sociobiology. The wildlife illustrator Sarah Landry "went beyond the effort required for an ordinary book on animal behavior, traveling to zoos and aquaria to sketch captive animals and visiting herbaria to render in detail the plant species found in natural habitats of the animal societies." (Wilson 1994, 324). In essence, the illustrator tuned her work to the naturalist's spirit of the book (Myers 1990).].

Wilson followed a similar approach when he included the notion of evolutionary stable strategies (ESS), recently developed by George Price and John Maynard Smith (in close relation to Hamilton), among the mechanisms of social evolution presented in the first chapters of *Sociobiology* (Maynard Smith and Price 1973; Harman 2010; Wilson 1975, 129). An “evolutionary strategy” designates a highly stylized representation of a type of animal behavior in relation to conspecifics or to the broader environment, limited to a small repertoire of options (such as fight or flight) with associated payoffs, measured in terms of fitness. It is denoted as “stable” if the individuals adopting it and largely present in a population cannot be replaced by individuals adopting a different strategy.

Drawn from game theory, an interdisciplinary theoretical framework developed since the 1940’s by mathematicians, economists and biologists to model social interactions (Erickson 2015), the notion of ESS facilitates the study of how populations composed of animals adopting competing types of behaviors evolve, through the resolution of mathematical models or through simulations. These advantages come at the price of a de-contextualization of the behaviors under study, and a difficult transposition of the assumption made on the rationality of the human players to a game played by animals.

The un-natural assumption of rationality led even mathematically inclined biologists like Richard Lewontin and Richard Levins not to pursue their initial interest in game theory for animal behavior studies (Erickson 2015, 221–22). In contrast, Wilson provided a stage in *Sociobiology* for a dialogue between game theoretic and naturalist approaches to animal social studies. Game-theoretic models need the scaffold of field observations, both for the calibration of their parameters (definition of the types of behaviors and of the payoff matrix) and to gauge their external validity, as witnessed by the references to a number of naturalist studies in the original paper on ESS by Maynard Smith and Price. The fact that game theory was integrated in a synthesis of animal social behavior studies under the authority of naturalists bolstered the relevance of the latter in the competitive landscape of contemporary biology.

Conclusion

Sociobiology: The New Synthesis has been extensively studied for the debate it initiated on the relationships between natural and social sciences. This concentrates the historical significance of Wilson’s book on one type of synthesis which the book claimed to achieve: the sociobiology of all social animals, from ants to human beings, developed in its twenty-seventh chapter. In this study, we put the focus on a different kind of synthesis pursued by *Sociobiology*, recasting it in the continuity of two scientific projects bearing such a name, which developed in post-war United States.

We argued that animal social behavior was investigated by ecologists, ethologists and comparative psychologists, each characterized by different practices of places. In these fields, researchers with an inclination for the collection of observations in natural conditions were feeling an increasing pressure to assert the legitimacy of outdoor studies, perceived not to meet the standards of rigor of modern science. Scott’s CSASNC, which morphed into the Section On Animal Behavior and *Sociobiology* (forerunner of the Animal Behavior Society), was an organizational effort explicitly directed at promoting studies of animal behavior wedding techniques and protocols from the laboratory and the field.

Altmann developed his own sociobiology project while observing primates for two years on Cayo Santiago Island, a type of field station which the CSASNC had called to develop for allowing observations blending natural and controlled conditions. Altmann's own version of sociobiology was still rooted in naturalist studies of animal behavior, but this time the deficit in legitimacy was not so much felt in relation to superior laboratory methods, than in regard to the reductionist program of molecular biology, which was so dominant in the immediate post-war period, especially at the Department of Biology at Harvard where Altmann was conducting his PhD under the sponsorship of Wilson. In this context, Altmann's sociobiology developed by combining extensive field studies with a heavy emphasis on the mathematical analysis of information and communication in animal groups.

In the light of these two preceding episodes, Wilson's sociobiology appears to follow a recurring pattern: the development of a defensive alliance between the naturalist approach to animal behavior studies and new forms of scientific endeavor threatening this naturalist tradition. While Scott was most concerned with laboratory settings replacing studies under natural conditions, Wilson risked to be sidelined by molecular biology, which favored sophisticated theoretical developments and a reductionist analysis of phenomena. Embracing these new developments by discussing them on par with classic studies of animal societies, as illustrated with the centrality of mathematical models of kin selection in Sociobiology, enhanced the relevance of the type of knowledge produced by naturalists: centrality of field work, attention to levels of social interaction at the group and interspecies level, and the study of evolutionary dynamics in broad, natural ecosystems [33: If a counterfactual can be sketched, an alternative to the sociobiology project can be imagined when considering the fate of Vero C. Wynne-Edwards, a prominent British naturalist convinced of the importance of group selection in animal societies (Wynne-Edwards 1962), not unlike Wilson. Contrary to Wilson, he kept an uncompromising stance against the reductionism and mathematical models of social behavior developing in biology. This led him to a position of complete isolation and quasi irrelevance in biology for decades (Borrello 2010).].

In this frame, the historical meaning of sociobiology can be reconsidered: in addition to the “bombshell” effect of the book *Sociobiology*, sociobiology as a series of post-war projects also represented a more discrete but effective attempt to reaffirm the relevance of the naturalist tradition in animal behavior studies and biology at large.

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