A Brief History of Primate Studies: National Traditions, Disciplinary Origins, and Stages in North American Field Research

Linda Marie Fedigan and Shirley C. Strum

The relationship of humans to our nonhuman primate relatives goes back almost as far as we can trace the human record in history and prehistory. Throughout this time and around the world, we have expressed strikingly diverse attitudes toward our primate relatives: we have eaten them as food, venerated them as deities and ancestral spirits, kept them for entertainment, portrayed them as symbols of evil and sin, seen them as comic imitations of ourselves, and used them as substitutes for humans in scientific study. Out of 3 million years of living alongside our primate relatives, it is only in the last 100 years, particularly in the 50 years since World War II, that humans have considered primates to be worthy of study in their own right. This science is sometimes called “primatology”—the study of the biology, behavior, ecology, and evolution of the prosimians, monkeys, and apes.

Even though the study of primates is relatively recent, the amount of research on primates is diverse. In this essay we will focus primarily on field studies of primate social behavior since 1950 in North America. Our objective is to trace some of the ideas about the nature of primate societies through different stages in the development of the discipline. To do this, we will outline the major stages and themes of each stage, as well as the key questions that have endured throughout the history of primate studies. And, to place this focused history into a larger context, we will begin by briefly describing how the study of primates arose in different places and how the major parental disciplines affected its development.

DIFFERENT NATIONAL TRADITIONS OF PRIMATE STUDIES

One of the unusual aspects of primatology is that it was independently and simultaneously invented at least twice in the 1950s, once by the Japanese and once by the Europeans and North Americans. Although they were aware of each other, Eastern and Western primatologists worked in relative isolation until the 1960s when translation of publications and visits to each other’s field sites facilitated communication. There were also somewhat independent origins of British, Continental European, East Indian, Chinese, North American, and South American primate studies, but these groups of scientists communicated with each other a good bit more from the beginning. The national traditions of primatology that began relatively late (East Indian, Chinese, South American) developed in the climate of global conferences and international journals that prevailed after the early 1970s and so were not as isolated as the early ones. And some of the earlier national traditions (British and European) developed in parallel out of the field of ethology and so shared similar origins. Still, it is possible to charac-
itize all of these national traditions as having had different histories and objectives, different influential figures and ideas, and different methodological preferences. At the risk of oversimplification, we will briefly introduce some of the distinctive features of several national traditions of primate studies.

Japanese primatology differs from Western primatology most clearly in its overriding emphasis on richly detailed descriptions of primate social behavior, its willingness to use anthropomorphistic interpretation, its emphasis on proximate mechanisms (immediate causes of behavior), and its training of young scientists by sending them into the field with few preconceived theories about how the animals should behave and how scientists should collect data. As Pamela Asquith (1986) has described, the fundamental assumptions about primates are different in Japan and in the West. In North America and Europe, our Judeo-Christian heritage, Cartesian-based science, and more recent history of behaviorism and sociobiological theory make us reluctant to infer mental states in animals—that is, to grant them an inner life that might be contiguous with our own. The Japanese, however, do not see humans as set apart in nature from animals and find it appropriate to attribute motivation, feelings, and personality to monkeys. Even the possession of a soul is not believed to be unique to humans. Thus, anthropomorphism, the attribution of human-like mental states to animals, is not taboo in Japanese primatology as it is in the West.

Another distinguishing feature of our intellectual heritage is that Western scientists have been more profoundly influenced by Darwinian evolutionary theory than have the Japanese. Thus, we tend to be more concerned with ultimate, evolutionary adaptive explanations than with proximate mechanisms of behavior. The founding fathers of Japanese primatology, Kinji Imanishi and Junichiro Itani, established several practices that were later adopted by some Western scientists, for example: provisioning the animals to habituate them to human observation; taking the time to recognize and name individual animals and to track their kinship relations; attributing personality to individuals and culture to groups of primates; and conducting cooperative long-term studies over many years to understand individual life histories, group traditions, and population trends.

Today, the channels of communication between Japanese and Western scientists are more open, and the two sciences are converging. Some Japanese primatologists use theories and methods borrowed from the West and, when they do, their papers are sometimes indistinguishable from those of Western scientists. In spite of the many differences between the origins of Japanese and North American primatology, one interesting parallel did exist—scientists from both traditions began their study of primates with the primary objective of better understanding human origins.

Research on primates began somewhat differently in Britain and Continental Europe. Rather than a search for the origins of human sociality, the European study of primates grew out of the fields of ethology (the naturalistic and evolutionary study of animal behavior) and ecology. Primates were seen as simply another set of species (albeit complex, long-lived species) in which to investigate the evolution, ecology, and mechanisms of behavior. Hans Kummer, who supervised a large number of the current generation of Swiss and German primatologists, was influenced by Heini Hediger, among other ethologists. Trained specifically as an experimental psychologist, Kummer taught his own students that hypotheses about primate behavior need to be tested through experiments as well as by collecting observational data. Kummer (1995) established a long-term field site to study hamadryas baboons in Ethiopia and set up colonies of hamadryas baboons and long-tailed macaques in Switzerland for captive research. Another influential European, who founded the “Dutch School” of primatology, is Jan van Hooff, who like Kummer was influenced by classical ethologists. Van Hooff studied under Desmond Morris in Britain (the latter a student of Niko Tinbergen) before returning to the University of Utrecht and establishing the colony of chimpanzees at Arnhem that have been the subject of much influential research. French primatologists, such as Annie and Jean-Pierre Gautier, were trained as ecologists and have been prominent in research on the guenons of Central and West
Africa, as well as establishing the captive colonies of *Cercopithecus* species maintained at the Paimpont Biological Station. The study of prosimians was also pioneered by French ecologists-zoologists, such as Arlette and Jean-Jacques Fetter and Pierre Charles-Dominique.

In Britain, Robert Hinde, John Crook, and K. R. L. Hall are generally credited with having founded the study of primates. Both Hinde and Crook were originally influenced by founding ethologists such as Niko Tinbergen and ornithologists such as David Lack. Hinde and Crook both began their careers studying birds before moving to primates and, eventually, to humans. Hall was a psychologist who carried out extensive and pioneering fieldwork on the terrestrial monkey species of Africa, such as patas, vervets, and baboons, but he died tragically early in his career. Hinde (1983) supervised a large number of the current generation of primatologists who are prominent in both British and American primate studies, and he established the “Madingley” colony of rhesus macaques for the study of mother-infant relationships. Hinde’s interest in infant development, and his distinction between three levels of social behavior (momentary interactions, long-term relationships, and the larger context of social structure), spawned a substantial body of diverse research on primate societies. His insistence on maintaining a balanced research program based on Tinbergen’s classic “Four Whys” (i.e., four types of questions about behavior: causation, ontogeny, function, and evolution) means that his students have addressed research questions at many levels.

Thus far, with the exception of Japan, we have outlined the origins of primatology in countries where nonhuman primates themselves are not indigenous. What about places in which prosimians, monkeys, and apes are native, so-called host countries? The growth of primate studies in Argentina, Brazil, Mexico, Kenya, Madagascar, India, China, and Thailand, for example, has been slower and more recent than elsewhere, primarily because these economically underdeveloped nations have different concerns to address, such as poverty, population, and development. However, there are fledgling sciences of primatology in these nations, and as one example we will very briefly outline the history of primate studies in Brazil.

The emergence of Brazilian primatology in the early 1980s can be traced to two major sources: laboratory studies of callitrichids (marmosets and tamarins) that focused on medically related topics as well as social behavior and field studies of monkeys that were motivated by conservation concerns. Although scientific interest in the monkeys of Brazil was originally stimulated by visiting European and North American researchers, a critical mass of Brazilian primatologists had formed by the mid-1980s and continues to grow. Emilia Yamamoto, a past president of the Brazilian Primatological Society, argues that Brazilian primatology is distinctive in drawing most of its students from the larger area of conservation research (rather than anthropology, psychology, or zoology) and in its strong focus on female relations, resulting from the prominent position of female monkeys in callitrichid social systems (Strum and Fedigan, in press a; Yamamoto and Alencar, in press).

**DIFFERENT DISCIPLINARY ORIGINS (1920–1950)**

If you attend one of the biennial meetings of the International Primatological Society, not only will you meet scientists from different nations around the world but you will also rub shoulders with researchers who come from many different disciplinary backgrounds. Primate studies are carried out by scientists affiliated with departments of anatomy, anthropology, biology, conservation, ecology, medicine, psychology, and zoology, to name a few. But it is fair to say that the study of primates in North America has had three major disciplinary sources—the fields of physical anthropology, psychology, and zoology.

In North America, systematic empirical research on the behavior of free-ranging primates was begun by the psychologist Robert M. Yerkes, who became interested in the study of great apes in the 1920s. In 1929 he and his wife, Ada, published a landmark volume, *The Great Apes*, summarizing all that was then known about these animals and calling
for more and better research on them. Yerkes established the first major American primate breeding and research laboratory at Orange Park, Florida, which was later moved to Atlanta, Georgia, and renamed the Yerkes Regional Primate Research Center. Yerkes also encouraged young students to go out into the field to study primates in their natural habitat. The most successful of Yerkes's students was Clarence R. Carpenter, who is considered an early pioneer of primate field studies. Although he had been trained originally to study pigeons, Carpenter developed many successful techniques for observing primates in the wild that are still widely used today.

Carpenter conducted several influential studies of primates in the 1930s, studying howler monkeys and spider monkeys in Panama and gibbons in Thailand. He described the howlers of Barro Colorado Island as living in relaxed, communal harmony, with groups held together by affiliation and mutualistic relations (Carpenter 1934). After trapping and shipping 500 rhesus monkeys to Cayo Santiago Island off Puerto Rico in 1938, Carpenter subsequently studied the sexual behavior of these macaques for two years prior to the outbreak of World War II. His main concern was to integrate social behavior with physiology through the study of social patterns such as sexual behavior, but he was also very interested in the dynamics and maintenance of social groups. He recognized the two-way interaction between field and captive studies—that it would be impossible to understand the data from captive studies without knowledge of the species in the wild, and that experiments under controlled conditions in captivity would help us to understand the patterns of behavior in the field.

The integration of field and laboratory research continues to be an important issue in primate studies today. There is a tendency for psychologists to be associated with laboratory studies of the "mind" in areas such as learning and cognition, but many primatologists trained in psychology also carry out fieldwork. Probably the most famous body of research in psychologically based primatology is deprivation studies, originally carried out by Harry Harlow, who trained many of today's leading researchers in laboratory studies of primate behavior, and whose infant deprivation research began as an accident. Trying to raise healthier monkeys for lab research, Harlow took infants away from their mothers at an early age. The results were surprising: these infants were psychologically, socially, and sexually disturbed. Thus began a series of experiments aimed at understanding the necessary elements for normal development in social primates (Harlow 1974).

Although Hugh Gilmore's (1981) historical analysis of primatology argues that zoologists had the easiest entry into primate field research because zoology already had a strong tradition in the naturalistic study of animal behavior, the fields of zoology and ecology were not as influential during the formative years of primate fieldwork in North America as were psychology and anthropology. Ecologists and zoologists did not have a special interest in primates per se and often found that shorter-lived species were more useful in exploring and testing evolutionary hypotheses. The relative contribution of these different parental disciplines has changed in recent years as scientists have begun to explore new ecological and evolutionary theories and models in the context of primate behavior (Southwick and Smith 1986).

Physical anthropology and anatomy were major sources of early interest in primate studies. Darwin himself devoted one appendix in his 1871 book, Sexual Selection and the Descent of Man, to a discussion of the anatomy or, more specifically, the "Faces and Hinder-ends" of primates. Two anatomists working in the 1920s who turned their research interests to primates were Adolph Schultz in the United States and Solly Zuckerman in Britain. Schultz established the measurement techniques that are still used in primate anatomy today, and Zuckerman is most remembered for his 1932 book, The Social Life of Monkeys and Apes. In it he proposed that female primates are continually receptive, that sexual bonds are the basis for primate society, and that dominance interactions between males over sexual access to females are a major force in primate social life. When Zuckerman conducted a study of the hamadryas baboons at the London Zoo in the late 1920s and early 1930s, the natural behavior patterns and social system of this
species were unknown. Today we know that hamadryas in the wild live in polygynous (one male, multifemale) social groups. This was not the case at the London Zoo at that time, where 100 adult males, strangers to each other, were put on an island with only 30 females. In the resulting chaotic fighting, many monkeys (and almost all the females) died. Zuckerman thought he was watching normal behavior, and he extrapolated from this human-induced catastrophe to a general theory that sexual competition must be the basis of primate social life. Although the first wave of field studies after World War II would disprove most of Zuckerman's conclusions, his book was very influential in generating primate research.

It was a later anatomist who had the greatest influence on the origins of primate field studies. In the early 1950s, Sherwood Washburn published a rationale for the naturalistic study of primates as part of anthropology, and he began to train a long line of anthropological primatologists who went on to train their own students and to form a school of thought that became a major force in North American primate research. Washburn's "New Physical Anthropology" (1951) moved beyond a merely static measurement of bones or dissection of cadavers to an adaptive view of anatomical features. To understand these anatomical adaptations, Washburn argued that physical anthropology must become the dynamic, holistic study of human evolution and behavior. An important part of the "New Physical Anthropology," in his view, was the study of our nonhuman primate relatives in their natural environments, and thus Washburn established the value of watching how primates actually behave in the wild.

STAGES AND ISSUES IN NORTH AMERICAN PRIMATE FIELD STUDIES

Having outlined how field studies of primates originated and varied from nation to nation, we now turn to a selected history of how primate field research has developed in North America since the early 1950s. To make this still immense topic more manageable, we will concentrate on one aspect: how and why our ideas about primate society have changed over time. When we examined the history of ideas about primate society (see Strum and Fedigan, in press b), we found that there were regularities in the way data were collected and interpreted. These regularities suggest that the study of primate society since World War II can be divided into four stages:

Stage One (1950–1965): The Natural History Phase
Stage Two (1965–1975): The Discovery and Dilemma of Variability Phase
Stage Three (1975–1985): The Era of Sociology
Stage Four (1985–present): The Advent of Behavioral Ecology

Even though these stages are somewhat arbitrary, they help us to illustrate changing themes, theoretical issues, and methodological practices.

We also found that throughout this history scientists have been interested in a fundamental set of questions about primate societies. These enduring issues may be differently phrased and variably answered in the various stages, but they remain the foundational, driving questions of the study of primate society:

1. Why do primates live in social groups?
2. What is the social structure of the group, and what holds society together?
3. What is the relationship of the group to its environment?
4. What are the roles of aggression, dominance, sex, and affiliation in primate societies?
5. What is the basic nature of males, females, and the relationship between the sexes?
6. What is the pattern of ontogeny, development, and socialization?
7. What are the roles of instinct, learning, and cognition in behavior?
8. What are the patterns of intra- and interspecies variability?
9. What is the evolutionary relationship between different social grouping patterns?

10. What is unique about humans, and what is shared with our primate relatives?

By showing how the answers to these questions change and shift, we can begin to gain a concrete sense of how the naturalistic study of primate behavior in North America has developed in response to new methods and theories, the accumulation of data, and the larger social and cultural context.

The Natural History Phase (1950–1965)

Prior to 1950, Zuckerman and Carpenter had both conducted research on the social behavior of primates. Among their concerns was why primates live in social groups. They had each resolved this issue quite differently. Zuckerman asserted that sex was the social glue and that male competition, expressed through competition and dominance, was the organizing principle. Carpenter's communal howlers, in contrast, stayed together through cooperation, affiliation, and mutual interest. These two foundational ideas were to lay dormant for nearly twenty years until the disruptive effects of World War II finally abated and a number of other factors converged to produce the first big wave of primate field studies in the early 1950s. Some of the factors that played a role in the dramatic surge of primate field studies at that time were Washburn's "New Physical Anthropology"; the Darwin Centennial Celebrations; restored funding for field research; renewed interest in primates as biomedical and evolutionary models; and improved technology (i.e., easier air travel to remote areas and better antimalarial drugs).

The rush was on to get out into the field and study free-ranging primates. Scientists from the United States, Britain, France, Switzerland, and Japan traveled to the tropical countries where prosimians, monkeys, and apes are found. Many primate species, such as baboons, patas, vervets, macaques, langurs, and lemurs, had never before been the objects of sustained and systematic research in their native habitats, and everything observed about them in the wild was new to science. The chimpanzees and gorillas that had eluded early attempts at naturalistic study were successfully observed during this stage by Jane Goodall and George Schaller, respectively. These first studies were very descriptive in nature and, much like early ethnographies in anthropology, covered a smorgasbord of topics: sexual behavior, maternal care, infant development, play, dominance hierarchies, ranging and feeding patterns, and territoriality. This can be termed the "natural history" phase of primatology because the major mandate was to collect descriptions of as many primate societies as possible using natural history methods.

Many of this first wave of primate researchers were trained as anthropologists and thus looked to the social sciences, especially to structural-functional models of human societies, for their interpretations. In structural-functional models, social behavior is seen as part of an ordered, integrated system in which individuals play patterned roles that function to fulfill the needs of the group. Washburn and his students were particularly interested in what came to be called the "primate pattern," basic adaptive features common across the order, and this framework helped us to understand human behavior and origins in an evolutionary context. In addition to anthropologists motivated by this agenda, biologists were also initiating important field projects in the 1950s. Some of these zoologists and ecologists returned to species and sites previously examined by Carpenter. For example, N. Collias and Charles Southwick returned to Barro Colorado Island to study howlers, Southwick went to India to study rhesus monkeys, and Stuart Altmann carried out a two-year study of the macaques that Carpenter had earlier transferred to Cayo Santiago.

Studies by two of Washburn's students can be used to exemplify this stage: Irven DeVore studied baboons in Rhodesia and Kenya, and Phyllis Dolhinow (formerly Phyllis Jay) studied langurs in North India. Although DeVore's reports described many different aspects of baboon behavior, his work is mainly remembered for its model of baboon society that emphasized male dominance, competition, and aggression (see DeVore 1965a). DeVore also collaborated with Hall to review baboon behavior
in several locations and several species and concluded that baboon society was remarkably similar across locations and environments. In contrast, Dolhinow described langur groups from North India as peaceful and relaxed, with the presence of infants as the major cohesive factor. Infants were readily passed between females who acted as “aunts” or babysitters, and although males helped to coordinate group movement, they were otherwise rather peripheral (Jay 1965, 1968). These two models of what maintains cohesion in primate society show a striking parallel to the earlier, pre-World War II models that had been proposed: Zuckerman’s baboon model (sex and dominance) and Carpenter’s howler monkey model (communality and mutualism). Thus, in stage one, the answer to the nature of primate society was still unresolved. However, Zuckerman’s theory that continual sex is the basis of primate society was seriously weakened when it was shown in this first wave of field studies that many primates have breeding and nonbreeding seasons.

In spite of the fact that many monkey and ape species were first successfully studied in the 1950s and 1960s, the predominant image of primates during this period was drawn from the idea that baboon society was structured around a male dominance hierarchy and relied heavily on male aggressive abilities. The subsequent baboon model of primate social life so captured the scientific and popular imagination, that baboons were often taken as representative of all monkey society, and monkey society was thought to represent all primate society, including that of humans. Popular interest in primates was intense after World War II as people looked to animals for answers about basic human nature. For example, researchers tried to determine the fundamental causes of aggressive behavior in animals in order to fathom what could give rise to aggressive levels so extreme in humans as to lead to global warfare.

The Discovery and Dilemma of Variability Phase (1965–1975)

Stage two is best characterized as the period that exposed the variability of primate behavior and society. The number of species that were first studied during this decade is too large to enumerate here, but these studies served to emphasize the differences among species and to challenge the notion that there was a unified “primate pattern.” It was, however, the reexamination of the same species in new locations that gave the most convincing evidence for the extent of variability in primate social and ecological patterns. During stage two, studies of baboons, vervets, chimpanzees, and langurs took place in different environments from the earlier research. The resulting descriptions of species behavior were diverse and often contradictory. This posed a major challenge to previous models and resulted in some skepticism about the usefulness of primate behavioral studies, particularly for anthropologists.

Studies of baboons and langurs during this period provide a useful illustration of the key themes and issues. In the late 1960s and early 1970s, studies of baboons in new locations by Thelma Rowell, Tim Ransom, Glen Hausfater, and Shirley Strum expanded and reevaluated parts of the stage one “male dominance” baboon model. For example, it was realized that females, not just males, had a dominance hierarchy and that females and their kin formed the core of the group since males transferred between groups. Even the importance of the male dominance hierarchy was questioned by Rowell (1974) and Strum (1982), and portrayal of the roles of males and females subsequently shifted.

During stage one, hanuman langurs had been studied by Phyllis Dolhinow (Jay) in North India, where they lived in multimale, multifemale groups characterized by peaceful, affiliative relations. A new study of these langurs in South India by Yuki-mara Sugiyama (1965) reported that they lived in groups containing only one male. Extra males lived in roving all-male groups that sometimes aggressively attacked the reproductive groups, defeating the alpha male and killing some of the infants in the group. Mothers who had lost their infants seemed to become sexually receptive soon thereafter and to mate with whichever of the new males had taken over leadership of the group. Following on the heels of the peace-loving langurs from the 1960s, this shocking finding did not seem to make sense. Existing theory, with its emphasis on a fun-
damental primate pattern and on a structural-functional model of society, suggested an interpretation of infant-killing as simply abnormal. But were the differences between the reports on langurs due to differences in the animals themselves, or to outside factors, such as observer bias?

Further evidence for other variations in social organization and behavior also raised the same question. Were the differences natural or artifacts? To reliably address this dilemma, better methods were championed. One way to reduce observer bias was to standardize the sampling of behavior and quantify the techniques used to collect data. Jean Altmann’s influential review (1974) and evaluation of sampling methods in animal behavior was published at this time. But even with better methods variability persisted.

If the differences were due to variation in the primates themselves (i.e., “real” differences), the question then became: What causes behavioral variation? There were two main types of interpretations available: phylogenetic and ecological. Differences found among species were attributed to distinctive evolutionary heritages, that is, to phylogeny. Differences within species were ascribed to ecological pressures that varied between locations or habitats. Perhaps DeVore’s baboons behaved differently from Rowell’s because he studied them on the open savannah and she studied them in the forests of East Africa. Perhaps Sugiyama’s langurs in South India were polygynous and aggressive because of the stresses of living near urban areas, whereas Dolhinow’s langurs in North India lived in more rural areas with a lower population density of both humans and langurs.

Thus, attention turned to the relationship of the group to its environment and to the ecological and evolutionary significance of different social grouping patterns. At first, encompassing ecological models were proposed to account for social patterns. For example, John Crook and Steve Garlan (1966) designed a model of “adaptive grades” of social organization where the species were sorted into one of five grades in relation to major environmental factors. This model failed, however, because there was as much variability within these “grades” as among them. However, this was the beginning of an improved ecological context for primate behavioral studies.

The Era of Sociobiology (1975–1985)

Thomas Kuhn (1970), an influential philosopher of science, argued that a science matures and changes not through the gradual accretion of knowledge and slow development of more accurate theories but by the quantum replacement of one overarching explanatory model (“paradigm”) with another. This he called a “scientific revolution.” These revolutions, or major shifts in thinking, occur when the existing paradigm seems increasingly unable to explain certain observations. Often, an outsider or outside theory then succeeds in invading this fertile terrain as scientists become convinced that they need another model to explain their observations. Although not everyone agrees with Kuhn’s thesis, it can be argued that something like a scientific revolution occurred in primate studies between 1975 and 1985. The Washburnian rationale for North American primate studies that had served the discipline so well since the 1950s began to falter. Two of its inherent assumptions were severely challenged: (1) that we can use the study of prosimians, monkeys, and apes to discern fundamental primate patterns that are also applicable to humans; and (2) that social science theories (e.g., structural-functionalism) can be applied to animal societies.

The major contender as a new explanatory model, or paradigm, for primate behavior was sociobiology. But sociobiology was not the only important contributor to organizing and interpreting ideas about primate behavior during stage three. At least four other factors played major roles: long-term studies began to bear fruit; new studies of previously unexamined species continued to provide exceptions and challenges to every rule; studies of female primates by women scientists challenged prior emphasis on males; and interest in cognitive theories emerged as Western scientists began to widely and seriously consider the possibility that animals, too, have minds.

The impact of sociobiology on primate research was revolutionary not in its insistence on an evolutionary framework but in its shift of the unit of
selection from the group to the individual and, ultimately, to the gene. The theoretical framework of sociobiology explains social behavior entirely in terms of self-maximizing, biological processes, the most important of which are self-replication and reproductive success. Thus, this model focused questions of adaptive behavior on the individual rather than the group or the species. Fitness now had two components—that which belonged strictly to the individual and that which reflected back on the individual through the success or performance of closely related individuals (kin). Altruism and cooperation were both transformed into selfish strategies that could be used to improve reproductive success under certain conditions, and behaviors that had seemed strange and abnormal before now acquired evolutionary interpretations. For example, infanticide was viewed by sociobiologists as an evolutionary tactic instead of an abnormality (e.g., Hrdy 1977a). This extreme act of aggression was seen as one way that an individual could improve its reproductive success at the expense of others. Aggression in general was also reinterpreted as an individual rather than a group tactic, and whether it was advantageous to be aggressive or cooperative was seen to depend on a range of factors in the social and ecological environment. In the sociobiological framework, variability among and within species was expected and believed to result from strong selection on individuals to employ a variety of strategically adaptive behaviors in specific local circumstances.

Space does not permit a thorough discussion of the impact of sociobiological thinking on ideas about primate societies, but in general sociobiology addressed and reinterpreted almost every dimension of primate behavior, including the nature of competition and cooperation, the importance of family and kinship, and the relationship between individuals (particularly parents and offspring), between males, between females, and between males and females. Sociobiology also changed the language of explanation. By combining economic language with game theory, many new metaphors were generated about “trade-offs” of “costs and benefits” and “the battle” of “tactics” and “strategies.” Three powerful subtheories of sociobiology—kin selection, reciprocal altruism, and parental investment—have all been applied to primate behavior. These theories, and their fundamental premise of self-maximization, and the linguistic metaphors of sociobiology have all been hotly contested within primatology. Nonetheless, primate studies flourished in this new intellectual environment (Gray 1985).

A second factor that revolutionized this stage was the rich information that began to come in from long-term studies of primates in the wild. Even though these studies had been under way for some time, it was only when they had lasted at least as long as the life span of the species under study, that is twenty years or more, that their full effect was felt (e.g., Goodall 1986; Strum 1987). The best known examples of such longitudinal projects are the studies of chimpanzees at the Gombe Stream and Mahale Mountains Reserves in Tanzania; gorillas at Karisoke in Uganda; orangutans at Tanjung Puting in Borneo; ringtailed lemurs at Berenty in Madagascar; Japanese macaques at Arashiyama and Takasakiyama in Japan; rhesus macaques on Cayo Santiago; baboons at Amboseli, Gilgil/Chololo, Gombe, and Mikumi; howlers at Barro Colorado Island; and muriquis at Caratinga in Brazil. All of these long-term projects share some crucial characteristics. Foremost is the identification of individuals and the tracking of genealogical lines. Individuals become much more than members of age and sex classes, and following them through their lives and the lives of their offspring produces rich detail and essential information on many topics. Longitudinal studies demonstrated the value of life history, demographic, and ecological data and provided evidence that behavior varies over time as well as across groups and species, suggesting that local history may provide as much an explanation for current behavior as ultimate selective factors.

During this stage, researchers also made a more sustained effort to study the truly hard to observe species—those living in the tops of the canopy, or active by night, or showing a preference for mangrove swamps, or relying on cryptic concealment. Despite the difficulties of obtaining information on the social behavior of these animals, the new studies on prosimians and New World monkeys did
yield some provocative results that challenged our generalizations based on the behavior of Old World primates. For example, the study of a substantial number of different lemur species raised the possibility that females may be dominant over males in most of this primate family (Jolly 1984). Research on the dispersal patterns of neotropical monkeys suggested that most species in the family Cebidae are female-dispersed, and that in some species, such as the muriquis and the spider monkeys, it is the males of a community that are related and closely bonded rather than the females, as in most Old World cercopithecines (Stier 1990).

Changing views of the cognitive abilities of animals also contributed to shifts in the images of primate society. Much earlier, Alison Jolly had argued for the central importance of social behavior in the evolution of primate intelligence, and Nicholas Humphrey had proposed that the large brain of primates was the result of adaptation to the complexities of social life. But it was really Donald Griffin (1976, 1984) who spearheaded a new movement to make animal “mind” part of the study of animal behavior, arguing that behaviorism had robbed animals of the cognitive abilities that were clearly essential to their survival.

Another prevalent theme of this stage was the study of female primates by women scientists. Although there had always been a number of women primatologists and many descriptions of female primates, the disproportionate influence of the baboon model, with its emphasis on male dominance and aggression, had sometimes made it seem as if females were unimportant. By the early 1980s women scientists began to change this view, some of them stating overtly that they were influenced by societal concerns over the Women’s Movement (Fedigan 1982; Hrdy 1984b; Small 1984). Female primates were documented to be important social forces in their groups, and this argument was synergistic with other stage three trends: sociobiological theory included an emphasis on female competitive strategies, long-term studies showed that female kin groups formed the core structure of many primate societies, and the changing view of animal “mind” implied that both males and females made strategic decisions.

By the end of stage three the idea that there might be one basic nature of primate society had been abandoned. Variability, documented over the past twenty years, had become enshrined in theory. Now, to answer the question “what is the social structure of the group, and what holds society together?” we have to first consider what species, what group, what habitat, and at what point in the group’s history.


Stage four is the hardest to characterize for several reasons. The most obvious is that it is our current history, and thus, still unfinished. But the difficulty of depicting the present stage is also the result of growing fragmentation and specialization within the discipline and increasingly complex interactions among theories, methods, and other intrinsic aspects of science, as well as between science and its larger social context.

The sociobiological decade ended with a number of new answers to old questions. Yet despite its unifying “self-maximization” premise, there were anomalous observations that presaged the trends of the present period. For example, social complexity in primates implied higher cognitive abilities that were not just “gene strategies.” And social strategies obviously involved cooperation and affiliation, as well as competition and exploitation. Stage four is perhaps best characterized as an era that has moved away from a strongly reductionist application of sociobiological theory. As it was used in the earlier decade, sociobiology emphasized genetic determinism. By contrast, the behavioral-ecological models favored in the present period espouse a more multicausal view of adaptation that emphasizes the interaction of ecological and social processes.

Behavioral ecology is primarily concerned with survival and reproductive strategies: how primates find enough food, avoid predators, and balance the conflicting demands their environment places on them. Both proximate and ultimate questions are asked about the ways in which animals interact with their living and nonliving environment. This broader perspective has placed greater emphasis on
the idea that primates are part of larger communities, which contrasts with previous approaches that treated each species separately.

As one example, behavioral ecology has taken a fresh look at why primates live in social groups. During stage four, primatologists have pursued a lively debate about the relative importance of enhanced predator protection (van Schaik 1989) as compared to the cooperative defense of resources (Wrangham 1987a) as the ultimate and primary benefits of group living. Obviously, the answer to why primates live in groups is multifaceted and involves a trade-off between increased predator protection and decreased foraging opportunities.

How groups function has also become important. Research has shown that, far from living a simple life, many primates are immersed in systems of social complexity based on diverse strategies of competition and defense. These depend on social skills, knowledge, and the creation and careful management of social relationships. What makes an individual successful goes far beyond its age, size, or strength. Social complexity implies cognitive as well as social skills. To use social strategies, animal actors have to perceive the multiple dimensions of relationships, to predict the combined effects of sequential or simultaneous polyadic interactions, and to plan and manipulate such interactions for their own ends. Thus, the study of dominance and other aspects of competition has advanced from a rather mechanistic model of "brute" force to an approach that parallels the study of human politics, with all its intricacies of motivations, objectives, manipulations, and deceptions (de Waal 1982, 1989). Research now focuses on phenomena such as alliances and coalitions, reconciliation, and how aggressive and nonaggressive strategies are integrated during an individual's lifetime (e.g., Strum 1994).

The cognitive revolution stimulated by the discovery of social complexity ignited an interesting controversy about the evolutionary origins of primate intelligence. The case for the social function of primate intelligence had been made much earlier, but this idea lay dormant for many years. Katie Milton revived the discussion by constructing an ecological hypothesis that focused on the need for primates to have cognitive maps for tracking seasonally available food resources essential to survival. Subsequently, the origins and evolution of cognitive abilities in primates has been explored by a variety of investigators (Byrne and Whiten 1988). In general, the social origins hypothesis for primate intelligence has had more advocates than the ecological origins model. As just one example, Dorothy Cheney and Robert Seyfarth (1990) used experimental playbacks of vocalizations to demonstrate that vervets not only recognize other individuals from their calls but can also recognize relationships between other members of the group, such as that between a mother and her infant.

During this stage, as previously, shifting geopolitics have affected research patterns. For example, studies of New World monkeys and Malagasy lemurs have flourished, in part because these areas are now open to foreign researchers and are increasingly stable, whereas many parts of Africa and Asia are closed to primate research because of political unrest. Two other ways in which the worlds inside and outside primate studies have converged are in the areas of animal welfare (animal rights) and conservation. The recognition of animal "mind" by Western scientists had unintended consequences for social action. The link between mind, awareness, and suffering provided the animal welfare movement with its primate agenda and made captive primates the most obvious candidates for "liberation." Animal welfare advocates alienated many scientists when they targeted all laboratory research involving primates, but, by raising their concerns, they also convinced many scientists to design their research to take into account the welfare and emotional well-being of the captive primates (Blum 1994). Animal rights have also been championed. In its most ardent statement, known as the Great Ape Project, a variety of scientists and others have argued that we should extend basic human rights to the great apes (Cavalieri and Singer 1993). Their argument is based on scientific evidence about ape minds, as well as the social complexity and language abilities of great apes. For animal rights activists, admitting apes into the human family is the first step in reconsidering the rights of many other species. At present,
this remains a very controversial and emotionally charged proposal.

Just as the line between science and advocacy is increasingly blurred in the arena of animal welfare and animal rights, so the line between basic and applied science has dissolved in the area of conservation. Although primatologists have always been concerned about the status of primates in the wild, no one is able to ignore the vulnerability of their subjects. Habitat destruction, medical research that relies on certain primate species, conflicts between farmers and primate "pests" throughout the developing world, the increased killing of monkeys and apes for "bushmeat" as logging penetrates deeper and deeper into tropical forest, and the attraction of primates as pets and for exhibition have all spelled disaster for already dwindling populations. It has become very clear that more and better techniques are needed to assess the status of vulnerable populations and to safeguard them. New techniques, such as the rapid assessment of population viability, and management tools such as reintroduction and translocation are the beginning of this new wave (Arambulo et al. 1993; Benirschke 1986; Western, Wright, and Strum 1994).

CONCLUSION

We have used changing ideas of primate society to illustrate how the discipline has changed over the last fifty years, a small window into the history of primate field studies. It is obvious that our understanding of primates is increasingly based on more information on more species in more environments. These data are both longitudinal and comparative among groups and species. Today, they include more ecology and biology than ever before. There have been important refinements in theory. Behavioral ecology, sociobiology, and cognitive ethology all present heuristic and intelligible frameworks for explaining the complexity that has been unearthed. Better methods of data collection, analysis, and modeling help us to agree on what constitutes data, even if we do not always agree on what the data mean. And, although many questions remain, no one could doubt that at the end of the twentieth century we have a better understanding of the diversity of primate societies and the reasons for this diversity than in the era of Zuckerman and Carpenter when field studies of primates first began.

ACKNOWLEDGMENTS

We would like to thank the participants of the 1996 Wenner-Gren conference in Brazil on "Changing Images of Primate Societies." These primatologists and science studies scholars from around the world expanded our horizons and increased our understanding of the multiple origins and different national traditions of primate studies. We also thank Sydel Silverman of the Wenner-Gren Foundation for Anthropological Research for supporting our inquiries into the history and nature of primate field studies. We gratefully acknowledge Rebecca Feasby for editorial assistance, and NSERC (Natural Sciences and Engineering Research Council of Canada) for funding LMF's research.