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Field Studies of Old World Monkeys and Apes

Recent prolonged field studies have led to radical revisions of our knowledge of primate behavior.

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For many years there has been interest in the evolutionary roots of human behavior, and discussions of human evolution frequently include theories on the origin of human customs. In view of the old and widespread interest in the behavior of our nearest relatives, it is surprising how little systematic information was collected until very recently. At the time (1929) Yerkes and Yerkes collected data for their book on the great apes (*1*), no one had devoted even one continuous month to the systematic study of the behavior of an undisturbed, free-ranging nonhuman primate. Apparently scientists believed that the behavior of monkeys and apes was so stereotyped and simple that travelers' tales or the casual observations of hunters formed a reliable basis for scientific conclusions and social theorizing. As a part of the program of the Yale Laboratories of Comparative Psychology, Yerkes encouraged a series of field studies of the chimpanzee (*2*), the mountain gorilla (*3*), and the howling monkey (*4*). These first studies proved so difficult that Yerkes could write, in the introduction to Carpenter's study, "His is the first reasonably reliable working analysis of the constitution of social groups in the infrahuman primates, and of the relations between the sexes and between mature and immature individuals for monkey or ape" (*4*, p. 4). Zuckerman, quite independently, had realized the importance of field observations and had combined some field work with physiology and the older literature to produce two very influential volumes (*5*). From this beginning, only Carpenter continued to make field studies of behavior, and his study of the gibbon (*6*) is the first successful study of the naturalistic behavior of a member of the family Pongidae. Hooton summarized (*7*) what was then known about the primates, particularly stressing the importance of behavior and the work of Carpenter and Zuckerman.

The war stopped field work, and no major studies were undertaken for some 15 years. Then, in the 1950's, investigators in Japan, England, France, Switzerland, and the United States independently started studies on the behavior of a wide variety of free-ranging primates. For the history of science it would be interesting to examine the reasons for this burst of parallel activity. Field studies were undertaken at more or less the same time, and publications start in the late 1950's and accelerate rapidly in the 1960's. This trend is still continuing and is well shown by the pattern of frequency of citations in a recent review by Hall (*8*). The review cites the papers of Bingham, Carpenter, Köhler (*9*), Nissen, Yerkes, and Zuckerman, but there are no references to additional field studies in the period 1941–1951, and most of the references are to papers appearing in 1960 or later.

The increased interest in primates, and particularly in the behavior of free-ranging primates, has given rise to several symposiums, and results of the new studies have been published almost as soon as they have been completed. Data from the recent field studies are included in volumes edited by Buettner-Janusch (*10*), Washburn (*11*), Napier and Barnicot (*12*), and, especially, DeVore (*13*). The volume edited by DeVore is devoted entirely to recent field studies and their evaluation. It includes accounts of the behavior of five kinds of monkeys, of chimpanzees, and of gorillas. Each chapter is by the person who did the field work, and in addition there are eight general chapters. Two new journals also are devoted to primates. *Primates*, published by the Japan Monkey Centre, is now in its 5th year, and *Folia Primatologica* has completed volume 3. Carpenter's field studies and general papers have been reprinted so that they are now easily available (*14*). Southwick has published a collection of readings in primate social behavior (*15*), and Eimerl and DeVore contributed a volume on the primates to the Life Nature Library (*16*). Field studies have recently been reviewed by Jay (*17*), and proceedings of a symposium organized and edited by Altmann should appear shortly (*18*). This abundance of published material makes it hard to believe that only 2 years ago a course on primate social behavior was difficult to teach because of the lack of easily available, suitable reading material.

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The New Field Studies

Obviously, with so much new data a complete review is impossible, and readers wishing more information and bibliography are referred to Jay (*17*) and to the symposiums previously noted. Here we wish to direct attention to the nature of the recent field studies and to a few of their major contributions. Perhaps their greatest contribution is a demonstration that close, accurate observation for hundreds of hours is possible. Prior to Schaller's field work, reported in 1963 (*19*), it was by no means clear that this kind of observation of gorillas would be possible; previous investigators had conducted very fragmentary observations, and Emlen and Schaller deserve great credit for the planning and execution of their study. A field study of the chimpanzee that seemed adequate in the 1930's now seems totally inadequate, when compared to Goodall's results (*20*). Today a field study is planned to yield something of the order of 1000 hours of observations, and the observer is expected to be close to the animals and to recognize individuals. A few years ago observations of this length and quality were thought unnecessary, if not impossible.

The importance of studies in which groups are visited repeatedly and animals are recognized individually may be illustrated by the problems they make it possible to study. For example, during one season of the year chimpanzees "fish" for termites by breaking off sticks or stiff grasses and sticking the prepared implement into a termite hole (*21*), and this whole complex of nest examination, tool preparation, and fishing is learned by the young chimpanzee. It can be seen at only one time of the year and can be appreciated only by an observer whose presence no longer disturbs the animals. Habituation to the observer is a slow and difficult process. Goodall reports (*20*) that after 8 months of observations she could approach to no closer than 50 meters of the chimpanzees and then only when they were in thick cover or up a tree; by 14 months she was able to get within 10 to 15 meters of them. The problem of tool use in nonhuman primates has been reviewed by Hall (*22*), but the essential point here is that the amount of throwing and object manipulation in the monkeys (Cercopithecidae) was greatly exaggerated in travelers' tales, which were uncritically accepted, and it took years of observation in a favorable locality to reveal the complexity of this kind of behavior in the chimpanzee (*23*).

Predation

Another example of the value of continued observations is in the study of deliberate hunting by baboons. In three seasons of field work and more than 1500 hours of observation DeVore had seen baboons catch and eat small mammals, but apparently almost by chance, when the baboon virtually stepped on something like a newborn antelope and then killed it (*24, 25*). But in 1965 DeVore saw repeated incidents of baboons surrounding, hunting, and killing small mammals (*26*).

The whole matter of predation on primates has been difficult to study. Rare events, such as an attack by an eagle (*27*) may be very important in the survival of primates, but such attacks are seldom observed, because the presence of the human observer disturbs either the predator or the prey. We think that the present deemphasis of the importance of predation on primates arises from these difficulties of observation and from the fact that even today most studies of free-ranging primates are made in areas where predators have been reduced or eliminated by man. Most predators are active at night, and there is still no adequate study of the nocturnal behavior of any monkey or ape. Predation probably can best be measured by studying the predators rather than the prey.

Recognition of individual animals is necessary for the study of many problems, from the first stages of the analysis of a social system to observations of social continuity or constancy of group membership; such observations are exceedingly difficult under most field conditions. For example, understanding of the dominance system implies repeated recognition of a number of animals under sufficiently various conditions so that the patterns of interaction become clear. Again, to be sure that a group has lost or gained a member, the observer must know the whole composition of the group.

Long-continued observations have proved to be important in many unexpected ways. For example, rhesus monkeys have been observed in several of their many very different habitats, and it has been found that young rhesus play more in cities than in some kinds of forest and play in the forest more at some seasons than at others. These differences are due in part to the amount of time which must be spent in getting food; the same forest troop may play more when fruits are available and hunger may be rapidly satisfied than at times of the year when the diet is composed of tiny seeds which take a long time to pick. Extracting the small seeds of sheesham pods during the months when rhesus troops spend most of their time in the sheesham trees takes many hours of the day (*28*). What might easily have been described in a short-term study as a species-specific difference of considerable magnitude turns out to be the result of seasonal and local variations in food source. It is essential to sample behavior in several habitats to gain an understanding of the flexibility of the built-in behavior patterns of a species, flexibility which precludes the need for development of new forms of genetically determined behavior to cope successfully with different habitats.

The long-term study in which many groups of a species are observed in different, contrasting localities, and in which at least some groups are known so well that most of the individuals can be recognized, will correct many false notions and will make valid generalizations possible. Although so far there have been only a few major investigations of this sort, some important generalizations seem possible.

Environment and Social Behavior

Nowhere is the extent to which the behavior of a species is adaptable and responsive to local conditions more apparent than among groups of rhesus living in India. Rhesus occur naturally in such diverse environments as cities, villages, roadsides, cultivated fields, and many types of forest ranging to altitudes of over 2400 meters. Contact with man varies in these habitats from constant and close to rare and incidental.

Where rhesus groups are subjected to pressures of trapping, harassment, and high incidence of infectious disease, groups are tense and aggression is high. These pressures are found in

areas where there is most contact and interaction with man, such as in cities and at places of pilgrimage. The animals are in generally poor physical condition, and numerous old and new wounds are evidence of a high rate of intragroup fighting. Tension among groups occupying adjacent areas of land is similarly high where there is insufficient space for normal movement and behavior, and where there may be intense competition for a limited supply of food and water. This is in sharp contrast to those groups living away from man where normal spacing among groups can be effected by the means evolved by the species. In the latter environments, such as forests, the rhesus are in excellent physical condition and what aggressive behavior occurs functions to maintain stable social groups and relationships among the members of the group; wounds are substantially fewer, and disease appears to be rare.

There has been considerable controversy in discussions of the relationships among social groups of the same species as to whether or not the geographical area occupied by a group should be called a territory or a home range. The point we wish to emphasize is that, within one species, populations living in different habitats may act quite differently toward neighboring groups. Populations may be capable of a wide variety of behavior patterns ranging from exclusive occupation of an area which may be defended against neighboring groups to a peaceful coexistence with conspecifics in which wide overlap in home ranges is tolerated. Because local populations of a species may maintain their ranges in different ways it is necessary to investigate all variations in group spacing in diverse habitats before attempting to describe characteristic behavior patterns for any species.

Not unexpectedly, population and group composition reflect these differences in habitat and stress. Groups living on the Gangetic plains, where trapping, harassment, and disease are important factors, are smaller, and the proportion of young members is also significantly smaller (*28, 29*). The long-term effects of pressures on different rhesus populations in northern and central India are now being investigated by a team of anthropologists of the National Center for Primate Biology.

A city presents a very different set of challenges to a rhesus group than does a forest. Often there are no trees to sleep in; living space must be shared with man and his domestic animals. Food is not available in the form common to other habitats, and monkeys may have to depend on their skill in stealing food from man. Often the food has been prepared by man for his own consumption, or it consists of fruits and vegetables pilfered from houses, shops, and streets. Garbage is picked through and edible portions are consumed. It is essential that the monkeys learn to differentiate between those humans who represent a real threat to their safety and those who are safe to approach. They must react quickly and learn to manipulate doors, gates, and other elements of the physical environment unique to their urban habitat. This is a tremendously different setting from that in which most rhesus live. City rhesus are more manipulative, more active, and often more aggressive than are forest rhesus. Clearly, the same species develops quite different learned habits in different environments.

Annual Reproductive Cycle

The belief, which has been widely maintained, that there is no breeding season in monkeys and apes gave rise to the theory that the persistence throughout the year of groups, or highly organized troops, was due to continuous sexual attraction. The evidence for a breeding season has been reviewed by Lancaster and Lee (*30*) who found that in many species of monkeys there is a well-marked breeding season. For example, Mizuhara has presented data (*31*) on 545 births of Japanese macaques of Takasakiyama. There were on the average approximately 90 births per year over six consecutive years. The average length of the birth season was 125 days, but it varied from 95 to 176 days. The majority of the births occurred in June and July. Copulations were most frequent in November to March and were not observed during the birth season, and in spite of this the highly organized group continues as a social unit throughout the year.

The birth season has been studied in other groups of Japanese macaques, and in general the situation is similar. There is no doubt that both mating and birth seasons are highly restricted in the Japanese macaque. The birth season is spring and summer, but its onset and duration vary considerably. If observations were limited and combined for the whole species, as they were in early studies, the birth season would appear to be much longer than in fact it is for an individual group, and it is the events within the local group, not averages of events for the species, that bear upon the role of sexual attraction in holding primate society together.

Under very different climatic conditions, in India, rhesus macaques also have a birth season, but copulations were observed in all months of the year, although probably not with equal frequency (*29*). Among rhesus on a small island off Puerto Rico births occur from January to June, and copulations are restricted to July–January (*32*). These data confirm the point that a birth season will be more sharply defined in a local group than in a species as a whole. There is a mating season among rhesus introduced on the island, but only a peak of mating in the same species in their native India (*29*). It is clear that survey data drawn from many groups over a wide area must be used with caution when the aim is to interpret the behavior of a single group. Since the birth season is an adaptation to local conditions, there is no reason to expect it to be the same over the entire geographical distribution of a species, and under laboratory conditions rhesus macaques breed throughout the year.

No data comparable to those for the macaques exist for other primates, and, since accurate determination of mating and birth seasons requires that reasonable numbers of animals be observed in all months of the year and that groups be observed in different localities, really adequate data exist for only the Japanese macaque. However, Lancaster and Lee were able to assemble data on 14 species of monkeys and apes. They found that probably the most common situation is a birth peak, a time of year at which births tend to be concentrated, rather than sharply limited mating and birth seasons. This is highly adaptive for widely distributed species, for it allows the majority of births to occur at the optimum time for each locality while maintaining a widely variable basic pattern. The birth season may be a

more effective adaptation to extreme climatic conditions. There may be a birth peak in the chimpanzee (*20*), and there may be none in the mountain gorilla (*19*), but, since we have no more data than are necessary to clarify the reproductive pattern in a single species of macaque, we can conclude only that, while birth seasons are not present in either gorillas or chimpanzees, a peak is possible in chimpanzees, at least for those living near Lake Tanganyika.

Prior to the recent investigations there was a great deal of information on primate reproduction, and yet as late as 1960 it was still possible to maintain that there were no breeding seasons in primates and that this was the basis of primate society. Until recently the question of seasonality was raised without reference to a birth season as distinguished from a birth peak, or to a limited mating season as distinguished from matings throughout the year with a high frequency in a particular period.

Frequency of Mating

Obviously many more studies are needed, and one of the intriguing problems is the role of potency. Not only does the frequency of mating vary through the year, but also there appear to be enormous differences in potency between species that are reproducing at a normal rate. In nearly 500 hours of observation of gorillas, Schaller (*19*) saw only two matings, fewer than might be seen in a troop of baboons in almost any single morning. The redtail monkey (*Cercopithecus ascanius*) mates rarely (*27*), but the closely related vervet (*Cercopithecus aethiops*) does so frequently. To a considerable extent the observed differences are correlated with structure (*33*), such as size of testes, and all these species seem to be reproducing at an adequate and normal rate. There is no evidence that langurs (*Presbytis entellus*) are less successful breeders than rhesus, but the langurs copulate less frequently (*34*).

Now that more adequate data are becoming available, the social functions of sexual behavior should be reinvestigated. The dismissal of the theory that sexual attraction is *the* basis of primate society should open the way for a more careful study of the multiple functions of sexual behavior. The great differences among the primate species should provide data to prove or disprove new theories. In passing it might be noted that the human mating system without estrous cycles in the female and without marked seasonal variations is unique.

Systems of Mating

Mating systems, like the presence or absence of seasonality in breeding and the frequency of copulation, are extremely variable in monkeys and apes. Eventually the relation of these variations to species adaptations will be understandable; at present it is most important to note that monkeys do not necessarily live either in harems or in promiscuous hordes as was once assumed. Restrictive mating patterns such as the stable and exclusive pair-bond formed between adult gibbons (*6*) and the harem system of the Hamadryas baboon (*35*) are comparatively rare. The most common mating pattern of monkeys and apes is promiscuity more or less influenced by dominance relationships. In species in which dominance relations are not constantly at issue, such as langurs (*34*), chimpanzees (*20*), or bonnet macaques (*36*), matings appear to be relatively promiscuous and are often based on the personal inclination of the estrous female. When dominance relationships are constantly at issue, as in baboons (*37*), Japanese macaques (*38*), and rhesus macaques (*39, 40*), sex often becomes one of the prerogatives of dominant rank. In such species dominant males tend to do a larger share of the mating than do more subordinate animals, but it is only in unusual situations that subordinate animals are barred from the mating system altogether. Mating systems probably support the general adaptation of the species to its environment. In most baboons and macaques the tendency for a few males to do much of the mating may be partly a by-product of natural selection for a hierarchy of adult males which dominates the troop so that in a dangerous terrestrial habitat external dangers will be met in an orderly way. Selection is not only for a male which can impregnate many females but it may also have favored a dominance-oriented social organization in which sexual activity has become one of the expressions of that dominance.

Dominance Relationships

Long-term field studies of monkeys and apes in their natural habitats have emphasized that social relationships within a group are patterned and organized in very complex ways. There is no single "monkey pattern" or "ape pattern"; rather, there is great variability, both among different species and among different populations of the same species, in the organization and expression of social relationships. A difference in the relative dominance of individuals is one of the most common modes of social organization in monkey and ape societies. Dominance is not synonymous with aggression, and the way dominance is expressed varies greatly between species. In the gorilla, for example, dominance is most often expressed by extremely attenuated gestures and signals (*19*); a gentle nudge from the dominant male is more than enough to elicit a submissive response from a subordinate, whereas, in baboons, chases, fights, and biting can be daily occurrences (*37*). In many primates there is a tendency for the major age-sex classes to be ranked in a dominance order; for example, in baboons, macaques, and gorillas, adult males as a class are usually dominant over adult females, and females are dominant over young. This may not always be true, for in several species of macaques some females may outrank some adult males (*36*), although groups dominated by a female (such as the Minoo-B troop of Japanese macaques) are extremely rare (*41*). Dominance relationships may be quite unstructured, as in the chimpanzee (*20*), where dominance is expressed in interactions between individuals but where these relationships are not organized into any sort of hierarchy. A much more common situation is one in which dominance relations, among males at least, are organized into linear hierarchies that are quite stable over time, as in baboons (*37*), langurs (*34, 42*), and macaques (*43, 44*). Sometimes these dominance hierarchies are complicated by alliances among several males who back each other up very effectively (*37*) or even by an alliance between a male and a female (*36*). Although dominance varies widely among monkeys and apes both in its form and function, it is certainly one of the most important axes of social organization to be found in primate societies.

Genealogical Relationships

Recognition of individual animals and repeated studies of the same groups have opened the way to the appreciation of other long-continuing social relationships in monkeys and apes which cannot be interpreted in terms of dominance alone. Long-term studies of free-ranging animals have been made on only two species of nonhuman primates, Japanese macaques, which have been studied since 1950 by members of the Japan Monkey Center, and Indian rhesus macaques living free on Cayo Santiago, Puerto Rico, the island colony established by Carpenter in 1938. In these studies, when the genealogy of the animals has been known, it has been obvious that genetic relationships play a major role in determining the course and nature of social interactions (*41*, *45–47*). It becomes clear that bonds between mother and infant may persist into adult life to form a nucleus from which many other social bonds ramify. When the genealogy of individual animals is known, members of commonly observed subgroupings, such as a cluster of four or five animals grooming or resting together, are likely to be uterine kin. For example, members of a subgroup composed of several adult animals, both male and female, as well as juveniles and infants, may all be offspring of the same female (*47*). These relations continue to be very important in adult life not only in relaxed affectional relationships but also in dominance interactions. Sade saw a female rhesus monkey divert the attack of a dominant male from her adult son and saw another adult female protect her juvenile half-sisters (paternity is not determinable in most monkey societies). There is a very high frequency of grooming between related animals, and many animals never seek grooming partners outside of their own genealogies.

It should be stressed that there is no information leading us to believe that these animals are either recognizing genetic relationships or responding to any sort of abstract concept of family. Rather these social relationships are determined by the necessarily close association of mother with newborn infant, which is extended through time and generations and which ramifies into close associations among siblings. We believe that this pattern of enduring social relations between a mother and her offspring will be found in other species of primates. Because of their dramatic character, the importance of dominance and aggression has been greatly exaggerated compared to that of continuing, positive, affectional relations between related animals as expressed by their sitting or feeding together, touching, and grooming. Much of this behavior can be observed easily in the field, but the extent to which it is in fact an expression of social genealogies has been demonstrated only in the studies cited above.

Positive, affectional relations are not limited to relatives. Male Japanese macaques may take care of young by forming special protective relationships with particular infants (*48*), but whether these males have any special relationship to the infants as either father or brother is uncertain, and the mating system is such that paternity cannot be known either to the observer or to the monkeys. MacRoberts (*49*) has recorded a very high frequency of care of infants by males in the Gibraltar macaque. In addition, he has demonstrated that these positive protective relations are very beneficial to the juvenile. Two juveniles which had no such close relationship were forced to be peripheral, were at a great disadvantage in feeding, and were groomed much less than other juveniles in the group.

The status of the adult can be conferred on closely associated young (frequently an offspring when the adult is female), and for this reason the young of dominant animals are more likely to be dominant. This inheritance of rank has been discussed by Imanishi (*45*) for the Japanese macaque and by Koford (*46*) for the rhesus. Sons of very dominant females seem to have a great advantage over other males both because their mothers are able to back them up successfully in social interactions and because they stay with their mothers near the other dominant animals at the center of the group. They may never go through the stage of being socially and physically peripheral to the group which is typical for young males of these species. A male cannot simply "inherit" high rank; he must also win this position through his own abilities, but his chances of so doing are greatly increased if he has had these early experiences of associating with and being supported by very dominant animals.

There could hardly be a greater contrast than that between the emerging picture of an orderly society, based heavily on affectionate or cooperative social actions and structured by stable dominance relationships, and the old notion of an unruly horde of monkeys dominated by a tyrant. The 19th-century social evolutionists attributed less order to the societies of primitive man than is now known to exist in the societies of monkeys and apes living today.

Communication

Research on the communication systems of monkeys and apes through 1962 has been most ably summarized and interpreted by Marler (*50*). Most of the data represent work by field observers who were primarily interested in social structure, and the signals, and their meanings, used to implement and facilitate social interactions were more or less taken for granted. Only in the last year or so have communication systems themselves been the object of careful study and analysis (see, for example, *18*). Marler has emphasized both the extraordinary complexity of the communication systems of primates and the heavy dependence of these systems on composite signals (*50*). Most frequently it is not a single signal that passes between two animals but a signal complex composed of auditory, visual, tactile, and, more rarely, olfactory signals.

Communication in some monkey species is based on a system of intergrading signals, whereas in others much more use is made of highly discrete signals. For example, most vervet sounds (described by Struhsaker, *51*) are of the discrete type, there being some 36 different sounds that are comparatively distinct both to the human ear and when analyzed by a sound spectrograph. In contrast, Rowell and Hinde have analyzed the sounds of the rhesus monkey (*52*) and found that of 13 harsh noises, 9 belonged to a single intergrading subsystem expressing agonistic emotions.

As more and more study is done on primates it will probably be shown that their communication systems tend to be of mixed form in that both graded and discrete signals are used depending on the relative efficiency of one or the other form in serving a specific function. In concert this use of both discrete and intergrading signals and of

composites from several sensory modes produces a rich potential for the expression of very slight but significant changes in the intensity and nature of mood in the signaling animal. Marler has emphasized (*50*) that, except for calls warning of danger, the communication system is little applied to events outside the group. Communication systems in monkeys and apes are highly evolved in their capacity to express motivation of individuals and to facilitate social relationships. Without this ability to express mood, monkeys and apes would not be able to engage in the subtle and complicated social interactions that are a major feature of their adaptations.

Social Learning

Harlow and Harlow's experiments (*53*) show the importance of learning in the development of social life; however, monkeys and apes are so constituted that, except in the laboratory, social learning is inevitable. They adapt by their social life, and the group provides the context of affection, protection, and stability in which learning occurs. No one factor can explain the importance of social behavior, because society is a major adaptive mechanism with many functions, but one of the most important of these functions is the provision of a rich and protected social context in which young mature. Field observations, although mainly observations of the results of learning rather than of the process itself, provide necessary clues as to the nature of the integration of relevant developmental and social factors. These factors can then be estimated and defined for subsequent intensive controlled research in a laboratory or colony.

It has become clear that, although learning has great importance in the normal development of nearly all phases of primate behavior, it is not a generalized ability; animals are able to learn some things with great ease and other things only with the greatest difficulty. Learning is part of the adaptive pattern of a species and can be understood only when it is seen as the process of acquiring skills and attitudes that are of evolutionary significance to a species when living in the environment to which it is adapted.

There are important biological limitations which vary from species to species and which do not reflect differences in intelligence so much as differences in specializations. For example, Goodall (*21*) has observed young chimpanzees learning to fish for termites both by their observation of older chimpanzees and by practice. It takes time for the chimpanzee to become proficient with these tools, and many mistakes are made. Chimpanzees are not the only primates that like termites, and Goodall has observed baboons sitting near chimpanzees watching and waiting while the latter are getting termites. The baboons are just as eager as the chimpanzees to eat termites but are unable to learn how to fish for termites for themselves.

It is likely that there are important variables among groups of a single species that make it possible for the acquisition of new patterns of behavior or the expression of basic learned species patterns to vary from group to group and from one habitat to another. For example, the nature of the integration and operation of a social unit vary in the extent to which it depends on the personalities of individuals in the group—this is another dimension of our understanding of how social behavior may affect species survival. Particularly aggressive adult males can make the behavior of their groups relative to that of adjacent groups with less assertive males substantially different. For example, a group with very aggressive males can control a larger geographic area than is occupied by a group with much less aggressive males. The tenor of life within a group may be tenser or more relaxed depending on personalities of adults in the group.

Imprinting has traditionally been distinguished from other learning processes by the fact that in imprinting the young animal will learn to follow, to be social (*54*), without an external or immediate reward (*55*). However, among monkeys and apes, simply being with other animals is a reward, and learning is reinforced by the affectional, attentive, supportive social context of the group (*56*). Butler was the first to use the sight of another monkey as a reward in psychological experiments (*57*). The field worker sees sick and practically disabled animals making great efforts to stay with their group. Among ground-living forms, animals that have lost or broken limbs or are so sick that they collapse as soon as the group stops moving, all walk along as the troop moves. Instances of wounded rhesus macaques' moving into langur groups after the rhesus have left or been forced out of their own group have been recorded. Clearly, it is essential for the young monkey or ape to mature in a social setting in which it learns appropriate skills and relationships during early years and in which it continues to learn during adulthood. "Where the individual primate is, in temporary isolation, learning a task without reference to any other member of its species, the learning is not normal" (*58*).

Future Primate Studies

At present many long-term studies are in process and major films are being edited (Goodall on chimpanzee and DeVore on baboon). There will be about twice as many major accounts available in 2 years as there are now. Since it is now clear that detailed descriptive studies of undisturbed free-ranging primates can be made, and since available data show that there are substantial differences in the behavior of the different species, more species should be investigated. So far studies have concentrated for the most part on the larger ground-living forms which are easier to study. There is no study of *Cercocebus*, little on *Colobus* (*59*), and nothing on the numerous langurs (*Presbytis*) of southeast Asia. New World monkeys have been investigated very little, and there are numerous genera that have not been the subjects of a major field study. Also, since local variation is important, forms such as the chimpanzee and gorilla should be studied in more and contrasting localities.

Once the general characteristics of the behaviors of several species are known, then interest can shift to topics such as detailed ecology, birth, infant behavior, peer groups, affectionate behaviors, sex, or dominance, to mention only a few. The behavior of a whole species is a large problem, and description has to be at a very general level when the goal is a first general statement. A problem-oriented study permits choice of species and elaboration of techniques. A further advantage of the problem-oriented approach is that it allows the close coordination of the field work with experimental work in the laboratory. Fortunately, no division has developed between those doing the field work and those involved in the experimental analysis of behavior.

Many scientists have done both controlled experiments and field studies. The interplay between naturalistic observation and controlled experiment is the essential key to the understanding of behavior (*60*). The character of the natural adaptation of the species and the dimensions of the society can be determined only in the field. Many topics, such as geographic range, food, predation, group size, aggression, and the like, can be seen only under field conditions. But the mechanisms of the observed behavior can be determined only in the laboratory, and this is the more complicated task. The relation of a field study to scientific understanding is like the relation of the observation that a man walks or runs to the whole analysis of locomotion. The field worker lists what the animals eat, but this gives no understanding of nutrition. The kinds of interactions may be charted in the field, but their interpretation requires the laboratory. Field workers saw hours devoted to play, but it was Harlow's experiments that showed how essential this activity was to the development of behavior. As the field studies develop it is to be hoped that they will maintain a close relation to controlled experiment. It is most fortunate that the present studies are being carried on by anthropologists, psychologists, and zoologists. An understanding of behavior is most likely to come from the bringing together of the methods and interests of many sciences, and we hope that the field studies remain a part of general behavioral science and do not become independent as workers and problems become more and more numerous.

Even now, in their preliminary state, the field studies can offer some conclusions that might be pondered by students in the multiplicity of departments now dividing up the study of human behavior. Behavior is profoundly influenced by the biology of the species, and problems of perception, emotion, aggression, and many others cannot be divorced from the biology of the actors in the social system. Early learning is important, and an understanding of the preschool years is essential to an understanding of behavior. Play is tremendously important, and a species that wastes the emotions and energies of its young by divorcing play from education has forfeited its evolutionary heritage—the biological motivation of learning. Social behavior is relatively simple compared to the biological mechanisms that make the behavior possible. Ultimately a science of human behavior must include both biological and social factors, and there is no more reason to separate the study of human behavior into many compartments than there would be to separate the field studies from the intellectual enrichment coming from the laboratory.

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