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A Survey of the Economic Systems of Wild Chimpanzees and Baboons

Frederic L. Pryor

In what ways are humans different from other animals? Various proposed indicators of the qualitative differences have fallen one by one as research in animal behavior has shown that nonhuman primates make and/or use tools, weapons, symbols, and other alleged accouterments of civilization. But even if we are unable rigorously to specify important qualitative differences between us and our closest animal relations, sufficient quantitative differences exist that it is worthwhile to investigate these phenomena along various dimensions, especially if we wish to understand something of the evolutionary journey that the human economy has taken.

The major purpose of this essay is to survey the economic systems of wild chimpanzees and baboons, primates featuring some marked differences in their social and economic life. Some pertinent comparisons of particular aspects of these economies will also be made regarding certain features of the economies of tribal peoples in order to gain perspective on human evolution.

Several limitations of this essay must be explicitly noted. First, the focus is primarily on observable similarities and differences of behavior, rather than on a general theory of ape and monkey psychology or decision-making mechanisms. Second, the discussion of empirical materials is limited to a cross-section analysis of different primate economies;

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it does not review the voluminous and confusing literature on the exact evolutionary path that has been taken.

The essay begins by specifying certain social and structural characteristics of these nonhuman primate societies. It then surveys materials from field studies concerning their economic systems by focusing on their production, distribution, and consumption activities. On the basis of this evidence, certain broader aspects of their—and our—economic systems are analyzed.

The Context of the Economic System

Biology and Geography

Chimpanzees belong to the great ape family, to the genus *Pan troglodytes*. Taxonomists differ on the specification of the various species, but with the exception of the pygmy chimpanzee (not considered in this discussion), the differences are small. They live in the wild only in sub-Saharan Africa, from Sierra Leone in the west across the Congo basin to Tanzania and Uganda in the east.

Baboons are old world monkeys of the *Cercopithecidae* family and genus *Papio*. Taxonomists also differ on the specification of the various species. Here, the focus is on only two types: the savanna baboon (which includes four subspecies) and the hamadryas baboon (sometimes called the desert or sacred baboon). Both types live in the wild over a broad area in sub-Saharan Africa and the tip of the Arabian peninsula.

The baboons have smaller brain sizes than the chimpanzees; when given problem solving tests allegedly measuring intelligence, they score lower [Rumbaugh and Gill 1973]. These tests, however, may not measure all relevant orders of intelligence.

Behavior and Environment

Because of the extreme adaptability of apes and monkeys, their behavior varies considerably in different environments. In captivity they may engage in certain sexual practices that have seldom if ever been observed in their native habitat. Chimpanzee behavior in laboratories can be remarkable: They have been taught certain symbols and have used these to obtain food; they also have been taught about money and may hoard the chips and take them from other chimpanzees by making threats.¹ Studies of such behavior in captivity may not show much about

activities in the wild, but they teach a great deal about behavioral potential [Kummer and Kurt 1965; Beck 1974].

Human interaction with primates in the wild also seems to modify their behavior. For all three groups considered here, there is evidence that provisioning (laying out food for them) evokes more aggressive behavior than is usual.²

It should be added that in the wild many characteristics of social organization also appear to be influenced by environmental conditions such as the size, clustering, and composition of the foraging bands of savanna baboons; employment of certain technologies; and diet. Although primatologists have made considerable headway in exploring such relationships [Altmann 1972; Eisenberg 1972; and Teleki 1977], much theoretical and empirical work still needs to be done before the underlying mechanisms can be fully understood.

The discussion below focuses only upon chimpanzees and baboons in their native habitats and relatively undisturbed by humans. The advisability of this limitation must be left to the judgment of the reader.

Social Organization

Of the nonhuman primates considered here, chimpanzees are the most "individualistic," using this word in a loose sense (and implying nothing about their personality). More specifically, they live in the forest in regional communities of roughly 30 to 80, but coordinated activity of the communities as a whole is relatively unimportant (even though coordination of subgroup activity occurs).³ Although members of the troop recognize each other and interact in a variety of ways in which they do not behave with nonmembers, these communities are apparently permeable to emigré chimpanzees (long-term census data are just beginning to be collected, for example [Teleki et al. 1976]). Chimpanzees travel in foraging groups of varying numbers, often very much smaller than the communities. The group may consist of a solitary chimpanzee, a mother and her infants or adolescent children, several adult males, or a mixture of these [Goodall 1965; for the somewhat different foraging pattern in another community, see Kosei 1970]. With the exception of a mother and her infants, these groups constantly form and reform. At night the chimpanzees sleep in trees in these small groups, but from one night to the next the group may change greatly in size and composition.

Several explanations for this loose social structure can be found in the literature. One is ecological. Chimpanzees eat a great deal of fruit from

trees that grow in small clusters in the forest, too small to provide food for more than a limited number. Chimp foraging groups are therefore smaller than those of nonhuman primates that eat roots and leaves, found in considerable quantity. Another explanation focuses on predation. Within the forest or semiforest environment in which the chimpanzees live, they need fear few predators; even a solitary chimp is in little danger of falling prey to some larger animal. An economic factor might be added. Although some economies of scale occur in chimpanzee productive activities, as noted below, it does not appear that such activities in large cohesive groups are necessary for survival. Thomas Pitcairn [1974, p. 267] notes that such a loose social structure is rare among nonhuman primates. The anthropological literature mentions a number of human hunting and gathering societies that feature fairly frequent fissioning and fusioning, but these processes occur much less often than among chimpanzees; and the units involved are usually small family units (and not, as occurs among the chimpanzees, single or unrelated individuals).

At the opposite extreme is the savanna baboon, which may be considered the most "collectivistic" of the groups discussed here, using this word in a very loose sense also. In most environments these monkeys travel together in troops of 30 to 80 members (occasionally numbering over 100); forage together as a troop; sleep together in neighboring trees (if these are not available, among rocks on a cliff); and fight together for mutual protection against predators. Sherwood Washburn and Irven DeVore [1963] note that most of a savanna baboon's life is spent within a few feet of others in its community, and in relatively rich environments this seems to be a good generalization. There is controversy among observers about the degree of permeability of these troops by nonmembers.

One explanation for such a social structure is the environment. The savanna baboon is preyed upon by many animals, including lions, leopards, cheetahs, and chimpanzees. By staying together, baboons are more likely to spot these predators. Furthermore, some adult males can help protect the females (who are much smaller) and infants while others drive away the enemy [Altmann and Altmann 1970]. I have been unable to find evidence in the anthropological literature of any human group that carries out so many activities together as a large unit. It should be added that the savanna baboons exhibit little division of labor, so that each is performing roughly the same activities side by side; thus, economies of scale in production do not seem to play a causal role in encouraging group activity.

The hamadryas baboon has the most complicated social structure of the species under examination [see, especially, Kummer 1968]. The basic

social unit is composed of an adult male, his mates, their infants, and some male adolescent hangers-on, designated in the literature as subdominant peripheral males. Ethologists call this basic group a one-male unit or, more picturesquely, a harem. Although the hamadryas spend most of their day in these smaller groups, the harems come together in troops of about 100 to 200 (sometimes as many as 750) to sleep. In the morning they start traveling together in small bands of 20 to 90, a unit that may fight with other bands. The troops appear to have an unstable composition, fluctuating considerably in size from night to night. A female adult hamadryas is very passive and under the coercive tutelage of her mate, who enforces his desires by a series of neck bites. In normal circumstances they are the only primates considered here who exhibit a fair degree of sexual fidelity (pair bonding); the others are sexually promiscuous [Kummer 1968]. Predation risks for the hamadryas are very much less than for the savanna baboons, primarily because they live in environments relatively inhospitable to predators.

Several interpretations of the hamadryas social structure have been offered. One is that the harem is adaptive for foraging in an arid environment. One large male is necessary for protection and insemination, whereas several would deprive the small females of food; grouping together to sleep is necessary because of the shortage of safe sites. Others have explained the banding together at night in terms of a genetic survival from the Ur-baboons, who faced environmental conditions similar to those still prevailing among savanna baboons. However valid these explanations, one cannot attribute such group activities to economies of scale in production, for these are unimportant.

The species examined here vary with regard to territorial behavior, that is, defense of an exclusive area or range by the troop. It is usually argued that territoriality is unimportant for chimpanzees, but in recent years one community has been observed to exhibit a form of territoriality. Whether this is due to special circumstances or to some general principle of chimpanzee social organization is not presently known.⁴ Among savanna baboons, observers have noted certain spacing mechanisms, also exhibited somewhat by the hamadryas. These mechanisms minimize conflicts between troops and are generally considered part of the territoriality phenomenon. Primatologists have noted that hamadryas baboons exhibit a confidence in claiming sleeping areas which is inversely related to their previous use of the site.

As is discussed below, both chimpanzees and baboons exhibit a certain sense of possession toward food. It should be emphasized, however, that neither territoriality nor possession of food or other goods [Kummer

1973, p. 83; Torii 1975] represents “property” in a significant sense. The crucial aspects of property are the procedures of enforcement that do not rely on physical force [see especially Pryor 1973, Appendix A-1], and these seem to be missing in the societies of our primate cousins.⁵

The social structures of the three groups considered here exhibit dominance hierarchies, as do those of most nonhuman primates [as surveyed by Jolly 1972, pp. 176–85; or Wilson 1975, chapter 13]. In some animal species, such as chickens, these hierarchies appear quite simple; the ordering is relatively transitive and stable, and the same hierarchy is manifested frequently and obviously in a variety of behaviors. Among the species of apes and monkeys under discussion, the dominance relations and mechanisms are quite complicated and subtle. These dominance hierarchies can affect the way they approach each other, their agonistic behavior (threats and fights), the distribution of food, troop conduct in defense against predators, and mating practices. Among chimpanzees, dominance relations depend not only upon the type of situation but also upon the individuals present [Lawick-Goodall 1975]. Dominance behavior occurs among them only rarely and is often difficult to observe; furthermore, even transitivity in such relations does not necessarily occur, and the hierarchy seems to differ according to circumstance [Reynolds and Reynolds 1965; Sugiyama 1973]. Dominance structures are much more evident among the baboons. Among savanna baboons, dominant males may defend the troop from predators; as is demonstrated below, this aggressive behavior has some important consequences for the operation of the economic system.⁶ A dominance hierarchy does not necessarily exhibit complete transitivity, and the literature is not in agreement [Hall and DeVore 1965; Hausfater 1975]. Among hamadryas baboons, dominance relations operate primarily between an adult male and his harem; dominance among males is apparent mainly when the band is deciding its direction of travel.

It should be added that nonhuman primates exhibit distinctive proto-cultures (adopting the approach and terminology of [Hallowell 1960]) among groups of the same species. The issue has often been debated and depends, of course, on one’s definition of the term. Assuming that *proto-culture* implies a socialization of the young, some type of communication, and a transmission of traditions, a number of observers [Lawick-Goodall 1973; McGrew 1978, 1977] provide evidence that social learning is considerable among monkeys and apes. Furthermore, if some entrepreneur in the society makes a discovery regarding production or consumption, it is often copied by others and transmitted to the next generation. Thus some communities of chimpanzees use special tools to collect termites, or leaf sponges for obtaining water from tree holes, or consume special

kinds of ants, while others do not. Certain baboon troops have special techniques for cracking nuts or for eating scorpions and snakes which others do not. Other aspects of a proto-culture, such as socialization of the young, have received considerable attention from many ethologists. Communication between nonhuman primates is the subject of an enormous literature and cannot be discussed here. Certain more strictly "cultural" phenomena have also been observed among chimpanzees. It should be clear that these proto-cultural or cultural components introduce difficulties into the analysis of behavior among nonhuman primates; among other types of animals, proto-cultural elements appear less important.

Economic Activities among Nonhuman Primates

Production

By *production* I refer to any activity (whether or not carried out consciously as production) that a conscientious national income statistician might include in the gross forest product of the species.

Obtaining food and making tools are the main forms of goods production among the primates under consideration. The chimpanzees and savanna baboons are omnivorous and may be considered nomadic (in the sense of having no permanent sleeping abode in their home range) gatherers and hunters. The overwhelming portion of their food (probably well over 90 percent) comes from either fruits and other vegetable matter or insects, galls, larvae, and so forth, obtained through gathering. The hamadryas baboons do not effectively engage in hunting and are solely nomadic gatherers.

These apes and monkeys also produce (perform) and exchange a number of important services. Grooming appears the most important economically, at least in terms of a portion of their time budget.⁷ Grooming is a type of skin care consisting of scratching, removing bugs, and cleaning wounds; it also has some social purposes. This service occupies several hours a day and should not be considered solely an activity of nonhuman primates; for example, Emanuel Ladurie [1978, chapter 8] has noted the daily hours spent in this important activity (especially for purposes of delousing) in Montaignou, a small French village of the fourteenth century.

Technology. Considerable evidence is available concerning how chimpanzees make and use tools [see especially Lawick-Goodall 1970; Teleki 1974]. They use grass stems to fish termites from their mounds; they also strip tree branches and carry them some distance for the same purpose.

Chimpanzees chew leaves and use the spongy residue to absorb water in tree openings or the remains in brain cases of recently killed game; they also use leaves for a variety of other purposes, including bandaging or wiping themselves. They use small sticks as toothpicks and rocks to open palm nuts. Young chimpanzees observe and learn about these tools and techniques from their elders so that a technological tradition is passed from generation to generation. Among other things, this means that chimpanzee technology varies markedly from one troop to another. Finally, it should be noted that chimpanzees sometimes use sticks and stones for defensive and offensive purposes [Eaton 1978; Plooi 1978].

According to Benjamin Beck [1974], "wild chimpanzees make and use tools with far greater frequency than wild baboons." Even when baboons and chimpanzees live in close contact, baboons do not appear to adopt chimpanzee technologies [Teleki 1974]. Some tool usage is reported; savanna baboons have been observed to use stones to open hard fruits and nuts [Jolly 1972, p. 351] and to dissect scorpions in order to eat them. They also dig holes on the sides of muddy rivers and drink the filtered water [Altmann and Altmann 1970, p. 157], an activity also seen among the hamadryas. Tool usage among the hamadryas appears almost nonexistent, but this seems traceable to social or perhaps environmental factors rather than genetic causes, for tool usage has been reported in one case of a captive hamadryas [Beck 1972].

Inventing and innovating activities of apes and monkeys have been observed. Jane van Lawick-Goodall [1971] has described her difficulties in setting up provisioning boxes, for the chimpanzees discovered quite easily how to open them and obtain food when they were not supposed to. An even more dramatic case occurred among a troop of Japanese macaques. One female discovered that the grain tossed on the beach by the human observers could be cleansed of sand by throwing everything into the water, letting the sand sink, and scraping off the floating grain. This technique later was adopted by her children and many other members of the troop [Kummer 1971, p. 122; see also examples in Wilson 1975, p. 170].

In summary, some species of nonhuman primates invent and employ new production techniques and tools; they also manufacture these tools and, to a certain extent, transport them for use. However, none of the nonhuman primates observed have developed techniques for food storage, and none of them seem to use tools to make other tools [Lawick-Goodall 1971, pp. 244–45]. In short, their technology remains at a very low level judged by conventional (humanocentric) criteria.

Production Cooperation and the Division of Labor. A division of labor

may not necessarily imply production cooperation, but it is useful to discuss these phenomena together.

Insofar as mutual defense is considered production, considerable division of labor can be observed. Among the savanna baboons, adolescent males act as scouts, and adult males serve as the main defense force when the troop is attacked. Among the hamadryas, the males protect the females. In some chimpanzee communities, males apparently patrol the home range boundaries and attack intruders from other communities. Although many other examples can be given, it seems most useful to focus the discussion of the division of labor and various forms of production cooperation on food production.

In all three groups under consideration, the primary production (foraging) unit is the single individual, and all but nursing infants forage for their own food. This does not mean that production cooperation or economies of scale in production are absent, as some have assumed.

An interesting sexual division of labor has been observed among chimpanzees while foraging. Males do most of the predation on mammals, while females do more exploitation of insect resources. Also, because adult females with infants are considerably less mobile than males traveling in small groups, the latter tend to forage over a much broader area. If they find a tree that is particularly rich in fruit, they may vocalize to attract other chimpanzees [according to Wrangham 1977, p. 527, these food calls are less frequent in times of food scarcity]. The less mobile chimpanzees can take advantage of the work of the more mobile, a feature of economic life that suggests certain economies of scale. (The degree of intentionality of such verbal messages is unknown but apparently is small; indeed, some [Hallowell 1960] have claimed that the only deliberate communication among nonhuman primates is nonverbal.) A sexual division of labor does not seem very important among the savanna or hamadryas baboons, who forage in groups [see, however, Rose 1978].

Cooperation in foraging and defense has been observed not only between members of the same animal species but also between members of different species. Eugene Odum [1971, p. 229] has labeled the phenomenon mutualism or obligate symbiosis (it may or may not be intentional). An important example is reported between savanna baboons and ungulates, such as impala [Washburn and DeVore 1963, p. 102].

In hunting, production cooperation and economies of scale are much more manifest. Considerable data have been collected about the chimpanzees, which have the most elaborate hunting techniques. According to Geza Teleki [1973], chimpanzees use three methods: seizing, chasing, and stalking. Seizing is opportunistic behavior (that is, the chimpanzee

grabs an animal that is close by) and can be carried out alone. Chasing and stalking involve groups of chimpanzees trying to corner their prey and require considerable coordination among the hunting team. A number of episodes have been recorded [see especially Teleki 1973] that testify to the complicated maneuvers. Teleki has noted [1973, p. 173]: "Chimpanzee predatory behavior is usually a collective activity that incorporates shared objectives and rewards." Although data collected about these episodes suggest that stalking is not particularly effective, group (as opposed to individual) chasing has a moderately high success rate and provides a nice example of economies of large-scale production.

Several aspects of this group cooperation should be noted. First, not all troops of chimpanzees employ these tactics; Toshisada Nishida [1979] studied a troop that used only rudimentary seizure techniques, which suggests that group hunting is not instinctual but is developed and socially learned by the troop. Second, such hunting may not be strictly traceable to hunger in a gross sense, for it sometimes occurs after the chimpanzees have stuffed themselves with other foods; any meat obtained represents luxury consumption unnecessary for survival in any narrow sense. (Given the probabilities of obtaining nourishment per calorie of effort expended, it may not be "rational" to hunt when one can forage.) Third, cooperative interaction among chimpanzees has been demonstrated many times in laboratory experiments, so cooperation may not be limited to hunting, although that is the most dramatic instance.

Among chimpanzees, coordinated hunting activity is carried on primarily by adult or adolescent males; females seem to hunt (apparently by seizing game) only when males are not present [Teleki 1973, p. 127]. The significance of this division of labor by age and sex is difficult to judge; as is discussed in detail below, females and infants do receive a share of what is obtained by the males, so their direct participation in hunting is not necessary to obtain meat. Similar division of labor and subsequent redistribution of product occur in a number of primitive human societies.

Hunting among the savanna baboon is more variable than among the chimpanzees. In some troops, meat eating is rare, only seizure techniques are employed, and only adult males hunt [Altmann and Altmann 1970; Washburn and DeVore 1963]. In other troops, meat eating is frequent, elaborate techniques such as relay systems are used, and adult males, adult females, and male adolescents hunt [Strum 1975].

Among the hamadryas, hunting has not been observed. However, this monkey is the least studied of the three under discussion, and much needs to be learned.

Production Functions. Although nomadic (in the sense noted above),

any given troop of chimpanzees or baboons occupies a relatively small range which it "harvests" through foraging activities. Among many species of nonhuman primates, there appears to be an observable relationship among troop size, richness of environment, and range; elaborate attempts have been made to propose testable hypotheses about these factors [for example, Altmann 1972]. For the species under discussion, however, there is considerable debate about the applicability of these ideas; so far, the generalizations made on the basis of empirical evidence have been rather simple (for example, in relatively poor environments, ranges are larger and troop sizes smaller). A more sophisticated approach to such questions has been made recently by Teleki [1977], who has attempted to analyze more carefully the spatial dimensions of chimpanzee society in terms of environmental factors and constraints.

Economic theory might lead us to a number of predictions about foraging strategies (for example, the use of extensive or intensive techniques). Unfortunately, the literature does not yield sufficient evidence to test these ideas, a problem compounded by the fact that (as discussed below) the objective function of the animals is unclear. We find only puzzles: Chimpanzees apparently range far in search of high energy foods, while purple-faced langurs (*Presbytes senex*) usually employ the opposite strategy and consume low energy foods that can be obtained without traveling very far [Hladik 1977]. Many primatologists are aware of this deficiency in the literature and are working on such problems.

Since none of these primates retain tools for any length of time, we can make one definite statement about the production function: Capital accumulation does not influence the long-run level or growth of production.

Distribution

By *distribution* I refer to those activities by means of which goods or services are enjoyed by those other than the producer. The various types of distribution are defined below strictly in behavioral terms; *reciprocity* refers to a situation in which ape or monkey A gives B some good or service X and receives the same in return; no reference is made to the intentions of the participants.

There is evidence that a certain amount of distribution through sharing and exchange occurs among chimpanzees in the wild, so that an incipient "norm of reciprocity" [as defined by Gouldner 1960] can be observed among them. Among the savanna and hamadryas baboons, in contrast, distributional activities are less evident for food and apparently less reciprocal for services.

Food. Among chimpanzees, distribution occurs primarily as a result of begging (a phenomenon also observed, although perhaps less frequently, in other animal species). Teleki [1973, p. 148] has classified four types of begging according to degree of success.

Although the literature focuses on the distribution of meat, distribution occurs for vegetable matter as well. W. C. McGrew [1975] provisioned chimpanzees with bananas and reports systematic observations of 457 transfers of bananas and 333 cases of unsuccessful begging. Of the successful transfers, 79 percent of the cases were mothers giving bananas to their children, 7 percent were children giving them to their mothers, 10 percent were adult males giving bananas to adult females, and 4 percent were miscellaneous or unspecified. Unfortunately, McGrew does not specify what percentage of the transfers were due to begging, taking, spontaneous giving, or other mechanisms. Such transfers are apparently less frequent for foods growing in nature, occurring primarily when infants and juveniles cannot open fruits with hard shells.

Chimpanzee distribution with regard to meat has attracted much more attention. It occurs less often and in a two-step sequence. The prey first is divided into several large hunks within two to four minutes after it is killed. Division is made by the chimpanzees who participated in the hunt plus others in the immediate vicinity. Any of these chimpanzees (for the most part, only males) can start pulling at it; it is, as it were, a public good. After this initial flurry of activity, however, the chimpanzees seem to recognize as possessors those holding large pieces (or the whole animal, if division has not occurred). In chimpanzee communities that do not engage in cooperative hunting, no such initial division of the meat that is individually caught has been observed [Nishida 1979].

The second step is the distribution of small pieces to others. Begging occurs, as well as snatching of the fallen food. Possession, not dominance, seems crucial at this point, and even more dominant chimpanzees will beg from the less dominant rather than take the meat from them. In communities where hunting cooperation is not practiced, rights of possession have not been observed to operate consistently, and incidents of a dominant chimpanzee taking the meat from another have been recorded [Nishida 1979].

Some statistical studies have been made of the receivers and givers of meat [see especially Teleki 1973, chapter 3]. Females in estrus are most likely to beg for meat from adult males, and their success rate is higher. Infants and adolescents beg from their mothers (who have, in turn, begged from the adult males); surprisingly (at least to me), their success rate is not markedly better than the average. Among the givers

of meat, the situation is quite simple: There is a fairly high but by no means perfect correlation between dominance and the chimpanzees that end up with large chunks after the initial division. The distribution of meat does not seem to reflect any strong reciprocity phenomenon (in the behavioral meaning given above); rather, dominant adult males usually give to those less dominant.

This transfer of food led Edward O. Wilson, a leading sociobiologist, to declare [1978, p. 151] that chimpanzees are, other than man, the most altruistic of all animals. This judgment may be overly enthusiastic. The female African hunting dog will carry meat to infants not even her own. If the statement is restricted to nonhuman primates, however, there is greater agreement among investigators. Primatologists have concluded: "Except for man and . . . chimpanzees . . . primates neither hoard food nor share it, except in the sense of allowing others to feed nearby. Even mother monkeys do not give up their food to their infants" [Jolly, 1972, p. 87].

Despite this praise for the chimpanzee, several *caveats* must be added. First, shared food apparently constitutes a very small portion of an average chimpanzee's diet. Second, during the provisioning periods when many bananas are available, dominant chimpanzees will keep the others from eating until they have had their fill. Finally, when they eat together, chimpanzees take food from baboons upon occasion, behavior that is not reciprocated, perhaps because the baboons are considerably smaller [Morris and Goodall 1977].

Neither the savanna nor the hamadryas baboon engages in food sharing through begging to any degree. Kummer [1968] reports that more dominant males sometimes displace less dominant ones from feeding grounds or eat grass plants that the latter have dug up; such displacement activities by baboons are difficult to observe because they require close attention to subtle movements. A number of observers report that male baboons take food from females or that mothers occasionally take food from their children, a behavior apparently rare among chimpanzees. If a savanna baboon obtains a small animal, others hover like vultures, waiting for pieces to fall or for the eater to become sated and leave the meat.

Among the hamadryas baboon neither food sharing nor food taking appears to occur. However, much remains to be learned.

Services. As noted above, nonhuman primates exchange numerous types of services, among which grooming occupies the most time for the species under discussion [time budget data for chimpanzees are found in Teleki 1977]. Since grooming can be provided by all but the youngest

infants, it seems useful to inquire about the reciprocal supply of services.

M. J. A. Simpson [1973, p. 434] shows that only about 25 percent of the average grooming sessions among adult male chimpanzees feature mutual grooming. He does show [p. 446] that, over time, the amount of grooming a particular male performs on any given partner roughly equals the grooming he receives. Data from Jane Goodall [1965, p. 469] reveal that among major social groups of adult chimpanzees (males, females in estrus, and other females) grooming accounts are roughly balanced. However, female adults groom infants and juveniles more than the reverse. A study of grooming behavior of chimpanzees in a zoo colony [Okono et al. 1973, pp. 94–95] showed that for every 100 grooming episodes (either grooming or being groomed), an average chimpanzee is likely to have an imbalance in its grooming account of about 23 (that is, it will be groomed 38.5 times and will groom 61.5 times, or *vice versa*).⁸ Although all these data are not comparable, my impression is that grooming reciprocity in the zoo is somewhat less balanced than in the wild.

The significance of these exchange data for the overall chimpanzee economic system can best be seen by comparing them to similar data for primitive human economies. Unfortunately, data for humans are very difficult to find, but in one economy, an Eskimo village with a strong ideological emphasis on reciprocity of exchange [Pryor 1977, chapter 4], similar calculations, for visiting and food sharing among adults, have been made. In comparison with the Eskimo (and employing a slightly different measure of nonreciprocity), the chimpanzees reveal greater reciprocity! Important nonreciprocities among the Eskimo are structured according to groups (for example, women are givers, men are receivers; married people are givers, unmarrieds are receivers; and so forth). Structuring in chimpanzee troops according to relatively formal subgroups does not seem very strong, so that this source of nonreciprocity does not arise.

Much less statistical evidence is available regarding grooming networks among savanna and hamadryas baboons. Qualitative evidence from the literature suggests that grooming reciprocity is much less balanced among the chimpanzees and that this nonreciprocity is highly structured. Among the savanna baboons, dominant males receive much more grooming than they give, especially from the females [Washburn and DeVore 1963; Washburn and Hamburg 1968, p. 471]. However, a female baboon is more likely to be groomed by a male if she is in estrus [Hall and DeVore 1965]. Among the hamadryas, most grooming occurs within the harem between the adult male and his mates; males seem to receive considerably more grooming than they give. Only very old or very young hamadryas

groom one another. It also seems that female mates of the same male do not groom one another very often. Hans Kummer [1968, pp. 44–45] reports that if a female is in estrus or if the number of females in the harem has declined, the adult male does a great deal more grooming than in ordinary circumstances.

Consumption

Chimpanzees and baboons spend almost all their time in foraging; food obtained from the dramatic kinds of hunting episodes discussed above represents a very small portion of their diet. This is not surprising, for most human hunting and gathering societies have found that food obtained from gathering is, relative to the effort involved, more productive and safer. Most of those societies obtain most of their nourishment from gathering [Lee 1968], and the reason apes and monkeys forage so much is undoubtedly the same.

The important role played by ecology in determining the types of foods consumed is shown by the considerable overlap in the lists of foods eaten by nonhuman primates and their human neighbors [Teleki 1975]. It should be noted, however, that neither group consumes all the available foods. McGrew [1977] presents evidence from experiment and observation in the wild that food habits among chimpanzees are relatively conservative; they do not readily eat new foods. Furthermore, foods consumed by different communities of chimpanzees in apparently similar ecological milieus vary, which suggests either that proto-cultural elements play a role or that the ecological factors are more subtle than have yet been discerned.

How important is this proto-cultural element in food selection? To answer this question we might investigate the nutrient value of the various foods, find out the minimum nutrient needs of these species, determine the relative scarcity of the various foods (which would represent a scarcity price of the foods), apply the standard linear programming techniques to solve the diet problem, and then compare the results with actual foods selected. Information about nutrient values is already available [for example, Hladek 1977], and other necessary data undoubtedly have been collected but not published. Short of an elaborate analysis, however, we can only rely on qualitative remarks by various primatologists, such as Hladek's observation [p. 500] that many foods selected have no obvious effect on nutrition.

Foraging in a group has certain disadvantages if the desired food grows in scattered patches. However, group foraging reduces the time each in-

dividual spends in defense or vigilance and so may increase the time available for searching for food.

Some Perspectives

The materials presented above can be analyzed from a number of varied viewpoints. For economists, three issues seem particularly important: the degree to which these primate species may be considered rational decision makers; the forces influencing their distribution of income; and the paths which led from their economies to ours.

On Economic Primate

Rationality, in a narrow sense, refers to choice. Nonhuman primates can be said to exhibit rationality or act economically if some of our models of rational choice can be applied to behavior of theirs that seems attributable to deliberate decision making. Of course, one must determine the degree to which they make deliberate decisions, in contrast to acting either instinctually or according to their proto-culturally learned patterns. Once a determination is made, one need not pay attention to their detailed reasoning processes, but may focus on their behavior.

Innovative behavior, by definition, involves deliberate decision making. Several examples have been presented above, and Melvin Fredlund [1975] has collected a number of others. But, unfortunately, available decision-making models do not apply to such creative behavior.

If we turn to other types of activities, a number of apparently rational nonhuman primate behaviors can be classified according to trade-offs. One is the labor-leisure trade-off. Stuart Altmann and Jeanne Altmann [1970, p. 90] have found that baboons sleep later in the morning when they are in richer gathering grounds (which they interpret to represent decision, rather than digestion). Another is the risk-production trade-off. The Altmanns present detailed evidence on baboons' geographical movements that shows they spend time in rich areas and avoid locales that do not yield much food or water; they frequent safe sites and avoid or spend little time in dangerous areas or activities; and they spend a moderate amount of time in rich but dangerous areas. Trade-offs also are made between different foods. Chimpanzees do not stuff themselves on the fruit of any given tree, but eat part of the fruits of one tree, move on to a different kind of tree, and return to the first tree another day [Reynolds 1965, pp. 162–63]. In terms of a production-consumption trade-off, chimpanzees have been observed cutting back on their gath-

ering activities when it is raining and uncomfortable to forage. Fredlund [1975] has collected a variety of material which illustrates the marginal principles that form the core of neoclassical economics.

The problem with this approach is that it does not tell us very much. In the cases mentioned, it seems that the nonhuman primates are engaged in making choices and that the results of their deliberations can be explained by models of rational decision making (if we impute a particular kind of utility function to them), but the imputation can be made only in certain special cases. To illustrate, two counter-examples to those given above will be presented.

Teleki [1973, p.57] noted that savanna baboons at the Gombe National Park would visit the feeding stations for the chimpanzees to obtain bananas, and in one year the chimpanzees killed 7 percent of one baboon troop and 9 percent of another. Nevertheless, the baboons continued to come; indeed, they even remained when the chimpanzees were busy eating one of their troop members [p. 153]. It may be that the utility of gaining bananas was considerably higher than the disutility of a 7–9 percent chance of being killed; or that information costs were sufficiently high that the baboons did not know the odds; or that the adults who made the decision to visit the feeding station were not the ones to be eaten (only infants suffered this fate). However, interpretations such as these fly in the face of evidence from Altmann and Altman [1970] and many other studies that savanna baboons are very sensitive to predation; after a predator kills a member of the troop, the baboons generally avoid the site for some time. Similarly, although there may be a certain utility to consumption variety, there are cases on record of both chimpanzees and baboons gorging themselves on the fruit of one tree the entire day. In this case a dedicated utility theorist would certainly argue that the utility of variety was less than the utility of the particular fruit, but this only tells us what we already know—the primates stayed by a single tree that day.

The problem is also illustrated in an interesting debate about the reasons (or the specification of the utility function) underlying predation activities among nonhuman primates. Various analysts have made reference to food crazes, troop traditions, pest-control of species competing for the same foods, complementary nutritional needs (to vegetable foods), environmental change, the desire to minimize energy expended per unit of energy obtained, and so forth. In the course of this heated debate, Strum [1976, p. 316] makes an interesting observation: “Most ecologists agree that optimization is likely a real phenomenon; few agree on just how it operates or at what level (the individual, population, or species). If

at the individual level, is it simply energy maximization or does it involve nutrient complementarity, use of time, fitness strategies involving intra-specific interference, and so forth? Optimization at higher levels, involving coevolution, interspecies interference, competition, or group selection may work against individual optimization, for example, making predators responsible (prudent) in their energy acquisition."

This debate reveals several methodological dangers. First, we should avoid conflating maximization with certain biological concepts. That is, Darwin did not speak of survival of the maximizers, but of the fittest; and it seems useful to separate short-run maximization from long-run survival. Second, until we have some better notion of the utility function of non-human primates (a matter in which revealed preference techniques might be applied), we must be cautious in our use of such concepts as function, adaptation, or utility maximization for primates. The analogues between this kind of methodological problem and, let us say, that arising in the analysis of enterprise behavior (at least some economists are unclear about whether maximization is occurring and what is being maximized) should be readily apparent.

Rationality, in a broader sense, refers to situations in which certain behavior contributes positively to some goal (implicit or explicit) of the society, such as its survival; but it is often unclear whether a deliberate decision is being made. For example, given the predator problem among the baboons, it seems rational for them to stay together for mutual defense. But two problems arise with this kind of analysis. First, it usually neglects the negative aspects of the behavior, for example, a large troop may not be able to find as much food for each individual as can monkeys foraging in smaller groups. Second, such arguments assume that it is possible to impute utility to certain "functions," but except for the survival case, this is very difficult to do in a convincing fashion without running severe risks of tautological argumentation.

Another illustration can be taken from Fredlund's [1975] analysis of the division of the hunting prey. He argues that the public good property of the prey during the first few minutes after it is killed is rational because it provides potential rewards for all participants in the cooperative venture. However, the baboons sometimes engage in violent free-for-alls, and some may be killed (which is dysfunctional, unless only the unfit perish). Furthermore, if the nonhuman primate participates in chase activities for sport, "property incentives" are unnecessary. Thus, designating the short period after the kill when the meat has no formal possessor as a rational public goods institution requires the imputation of motives about other aspects of the hunting process for which we have no information.

I am not trying to deny the usefulness of the utility maximization model. But applying it as an *ex post* explanation for various aspects of chimpanzee and baboon life may obscure, rather than illuminate, the casual forces that may be involved in bringing about adaptive behavior on any level.

On Exploitation and the Distribution of Income

For *exploitation* I do not use the Marxian meaning that stems from the ownership of the means of production and the extraction of surplus value; I use the neo-Marxist meaning of "unequal exchange." The distribution of income (more specifically, differences in consumption levels) can be influenced by both the distribution of production and by unequal exchange.

The distribution of production in any foraging economy is affected by the ability of the gatherer to cover a wide area. Among chimpanzees, the necessary vigor to do so may be reinforced by the extra food obtained (as long as the marginal unit of energy expended is less than the energy obtained). Since physical vigor is also positively related to dominance, which is related to obtaining meat during its initial division, the more dominant chimpanzees produce more and are in a position to consume more. Among baboons, which forage in groups, such differential production is probably less important.

In the context of the economies under study, equal exchange is illustrated by the reciprocal exchange of services among chimpanzees. The watchword seems to be: "Scratch my back and I'll scratch yours." We can approach the question of exploitation more systematically by reviewing the various types of unequal exchange, and an obvious threefold classification suggests itself.

The first type may be designated "altruistic transfers" (in this phrase, altruism refers to behavior, not motive) and consists of the producer giving food to those who did not participate in its production. This behavior, which occurs only among the chimpanzees, is a process by which the distribution of income is made more equal, since the possessors of such food generally have a higher consumption level.

The second type of unequal exchange is the taking of food from the producer. This is usually carried out by the dominant over the less dominant and represents a regressive transfer since the dominants have a higher real income in terms of consumption of goods and services. This malevolent transfer does not seem to occur often among the chimpanzees, except in rare circumstances when dominance hierarchies become especi-

ally important (for example, zoo settings or artificial provisioning). Among savanna baboons, these unequal exchanges occur somewhat more often, as when males take food from females or less dominant baboons are displaced from feeding grounds. However, one receives the impression that only a minuscule percentage of total food consumed is involved, especially in contrast to human gatherers and hunters [some quantitative evidence is available in Pryor, 1977]. Among the hamadryas, malevolent transfers of food seem extremely unimportant.

The third type of unequal exchange is represented by grooming services that are not fully reciprocated (in a behavioral sense). This also seems to be a regressive transfer since the dominant primates usually receive and the nondominant give. (The nondominant may groom the dominant in order to receive protection later.) This situation occurs primarily among savanna and hamadryas baboons, especially with regard to the grooming of males by females. Such exploitation based on sex is not unknown among humans; in Montaillou, the fourteenth-century French village referred to earlier, adult men were much more often deloused by adult women than vice versa [Ladurie 1978, chapter 8].

In human societies with very low levels of economic development, the leaders of the group often are net food givers to the others; indeed, this is a means of establishing their leadership [Pryor 1977, chapter 10]. It is only in economically more developed societies that dominance is reflected in greater receiving than giving. In this respect, the chimpanzees are similar to the most primitive human societies, while the savanna and hamadryas baboons are more similar to advanced human societies. Such a paradoxical result suggests some of the dangers of making evolutionary inferences from current data on different species of nonhuman primates. Further complications in the analogy arise when other primates, such as rhesus monkeys, are considered. In some cases of experimentally induced famine, the dominant rhesus monkeys will take food from the less dominant (which become lethargic); through this mechanism, the "best" genes are preserved.

The fact that dominance is reflected in nonequivalent exchange of a regressive type is not necessarily maladaptive, no matter how abhorrent it may be on an ethical level. Among the savanna baboons, the dominance hierarchy also yields an important defense function which benefits all of the less aggressive. The hamadryas male also plays a similar protective role for the females in his harem, although the need for protection appears considerably less than for the savanna baboon. To draw a human analogy, in wartime we often feel generals may be obnoxious and greedy, as long as they are successful; indeed, in extreme situations, only the most ag-

gressive and unpleasant people make the best generals. (It should be added that counter-examples can also be given.)

Dominance can appear in situations in which it does not seem to have any important relation to survival or any other positive function of the society, for example, in provisioning situations or in zoos. In these cases, the unequal exchange engendered by dominance is more difficult to justify. The extreme plasticity of the chimpanzees regarding exploitation (benevolent transfers and reciprocal exchange in one type of situation; dominance and unequal exchange in others) is a behavior pattern whose strands have not yet been completely separated, a puzzle upon which to end our meditation on this subject.

On Long-Term Economic Change

Even the most primitive human hunting and gathering societies feature considerably more complicated social structures, more developed divisions of labor, and more extensive cooperation at different levels than those of the nonhuman primates under discussion. Human societies have much more sophisticated production technologies. This is especially true for hunting; humans have devised various kinds of traps, weapons, and stalking techniques, observed only in the most rudimentary form among our primate cousins. Food preparation technologies, especially cooking, are considerably more advanced among humans. Interestingly, food storage techniques are almost nonexistent among some human societies living in environments similar to those of the monkeys and apes, so differences do not appear as striking along this dimension. Humans do seem willing to abstain from eating certain food that has been gathered so as to provide a small—but perishable—emergency stock. Apes and monkeys apparently do not do this, although occasionally chimpanzees eat only part of the fruit in a tree and return another day to finish it, and they sometimes carry meat around for several hours, rather than consume it on the spot (perhaps because they have no safe place to store it).

In the sphere of distribution, statistical analysis by Pryor [1977] has shown that three types of exchange and transfer (modes of distribution) exist in human hunting and gathering societies. Each type accounts for distribution of about 5 percent or more of goods and services produced in the economy: the reciprocal exchange of goods; the reciprocal exchange of services; and (benevolent) transfers of goods. Neither chimpanzee nor baboon economies appear to feature the first type. Although the second and third modes occur in chimpanzee economies, the magnitude of the transfer of goods seems to be very much smaller than in the human socie-

ties. Baboon society mainly features the reciprocal exchange of services, although baboons also transfer services (nonreciprocated grooming), a mode of distribution which usually occurs in human societies only at considerably higher levels of economic development.

All in all, it appears that the differences in human gathering and hunting economies and the economies of the nonhuman primates under consideration lie more in the sphere of distribution (exchanges and transfers) than in production (gathering and hunting). Unfortunately, distribution in primate societies has been studied less intensively than production, and many years of patient, difficult, and uncomfortable fieldwork by primatologists is necessary before judgments on such matters can be made with more certainty.

The big puzzle is the path of evolution over the last few million years. Here, two serious methodological problems arise. First, we cannot deduce very much about dynamics from the comparative statics analysis that has been performed, a problem well known in economics. Second, the similarity of certain economic features does not connote evolutionary closeness. For example, in an interesting comparative analysis of the societies of a large number of carnivores and of nonhuman primates, Philip Thompson [1975] shows that the former are more similar to humans along a number of dimensions than are the latter (in terms of food storage, division of labor, killing more game than is needed to eat, food sharing, and so forth). Since the carnivores studied are considerably more distant from humans in intelligence and anatomy than the nonhuman primates, the lesson from such a comparison (even though some details can be disputed) should be taken seriously.

Given these methodological difficulties—and others—it should come as no surprise that disagreements among biologists about the path of evolution from the Ur-primate to humankind are intense. Furthermore, some of the mechanisms that promote survival of a species may relate to dominance and strength, while others may relate to cooperation. It is difficult, if not impossible, to specify which of those mechanisms played an important evolutionary role when humans and nonhuman primates split in their evolutionary development.

Concluding Remarks

Much about the economic life of chimpanzees and baboons remains unknown. Certainly, the Chicago School economist would wish to know more about information and transaction costs; the Marxist, more about dominance and exploitation; the production theorist, more about the

ecological conditions defining the production function; and all of us, more about exchange and transfer. We are many decades from being able to construct convincing mathematical models of these economic systems in the manner that, for example, Wilson [1975, chapter 14] has done for social roles in an ant colony.

What use are studies of nonhumans for economists? On the most immediate level, some may illuminate facets of human gathering and hunting societies, particularly their ecological adaption [for example, Teleki 1975]. Such investigations also may help us answer a more basic question of a different order: Who are we, and from whence have we come? But we need other kinds of knowledge to answer another question: Where are we going, and what are we to become?

Notes

1. Such hoarding and seizing behavior among chimpanzees has been observed only in very attenuated form in the field. Designating the taking of money tokens as "stealing" is incorrect, since it implies a sense of property which may not be present. These laboratory experiments have been described by John Wolfe [1936] and have been observed in a variety of other experiments since then.
2. Evidence for chimpanzees is described by Jane van Lawick-Goodall [1971] and Geza Teleki [1973]; for savanna baboons, see Ueli Nagel [1974, p. 173]; and for hamadryas, see Hans Kummer [1968, p. 6]. This phenomenon receives various contradictory interpretations.
3. Coordinated subgroup activities include patrolling and hunting. Concerning the entire group, there is considerable controversy [see Pitcairn 1974] about the exact social role of the chimpanzee community and whether the community is a social unit. Those arguing the affirmative include Goodall [1979] and Teleki [1977]; those holding opposite views include Vernon Reynolds and Frances Reynolds [1965].
4. In the early 1970s the allegedly gentle troop at the Gombe National Park split into two groups. Sometime thereafter the larger group began to attack the smaller, and eventually the smaller community was effectively decimated [Goodall 1979]. Interpretations of this phenomenon vary considerably.
5. Although territoriality is not equivalent to a sense of property in the strict sense, some of the economic analysis concerning property can be applied to it; see the interesting article by Melvin Fredlund [1976]. Discussions about animals' territorial imperative provide dubious explanations for human behavior until it can be demonstrated that the meaning of such activity is interpreted similarly by the various groups being compared. Otherwise, the comparisons are merely a behavioral parallel upon which to meditate.
6. The link between external defense and internal dominance behavior in

the group is, of course, aggressive activity; thus, this complex of external and internal behaviors exhibits a consistency that has impressed many observers. Parallels with human societies usually leave something to be desired in the way of rigor or meaningfulness.

7. A number of serious conceptual difficulties arise in defining *services* in economic terms, some of which have been explored [Neale 1964; Pryor 1977, pp. 26–27]. Although I am not sure that social grooming would fit into the definition proposed by either of these sources, this activity occupies roughly 19 percent of the waking hours of the chimpanzees at Gombe and considerable amounts of the baboons' time. Without worrying about a precise definition of *service*, I stretch the concept in this essay to include grooming.
8. These data are for the grooming accounts for individuals in the aggregate; greater imbalances appear between individual pairs of chimpanzees. When grooming is scored according to quality (length of time, and so forth), the accounts are somewhat more unequal.

References

- Altmann, Stuart A. 1972. "Baboons, Space, Time, and Energy." Philip J. Clark Memorial Lecture. May 18.
- Altmann, Stuart A., and Jeanne Altmann. 1970. *Baboon Ecology: African Field Research*. Chicago: University of Chicago Press.
- Beck, Benjamin B. 1974. "Baboons, Chimpanzees, and Tools." *Journal of Human Evolution* 3 (November): 509–16.
- Beck, Benjamin B. 1972. "Tool Use in Captive Hamadryas Baboons." *Primates* 13 (September): 276–96.
- Clutton-Brock, T. H., ed. 1977. *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes*. New York: Academic Press.
- DeVore, Irvén, ed. 1965. *Primate Behavior: Field Studies of Monkeys and Apes*. New York: Holt, Rinehart and Winston.
- Eaton, Randall L. 1978. "Do Chimpanzees Use Weapons or Mimic Hominid Weaponry?" *Carnivore* 1 (May): 82–89.
- Eisenberg, J. F., et al. 1972. "The Relation between Ecology and Social Structure in Primates," *Science* 176 (26 May): 863–74.
- Fredlund, Melvin C. 1976. "Wolves, Chimps and Demsetz." *Economic Inquiry* 14 (June): 279–90.
- Fredlund, Melvin C. 1975. "The Economics of Animal Systems." In *Frontiers of Economics*, edited by Gordon Tullock. Blacksburg, Va.: University Publications.
- Goodall, Jane. 1979. "Life and Death at Gombe." *National Geographic* 155 (May): 593–620.
- Goodall, Jane. 1965. "Chimpanzees of the Gombe Stream Reserve." In DeVore [1965]. Pp. 425–73.
- Gouldner, Alvin W. 1960. "The Norm of Reciprocity: A Preliminary Statement." *American Sociological Review* 25: 161–79.

- Hall, K. R. L., and Irven DeVore. "Baboon Ecology." In DeVore [1965]. Pp. 20–53.
- Hallowell, A. Irving. 1960. "Self, Society, and Culture in Phylogenetic Perspective." In *Evolution after Darwin*, edited by Sol Tax. Vol. 2, *The Evolution of Man*. Chicago: University of Chicago Press. Pp. 309–73.
- Harding, Robert S. O. 1975. "Meat Eating and Hunting in Baboons." In *Socioecology and Psychology of Primates*, edited by Russell H. Tuttle. The Hague: Mouton. Pp. 245–57.
- Hausfater, Glenn. 1975. *Dominance and Reproduction in Baboons (Papio cynocephalus)*. Basel: S. Karger.
- Hladek, C. M. 1977. "Chimpanzees of Gabon and Chimpanzees of Gombe: Some Comparative Data on Diet." In Clutton-Brock [1977]. Pp. 481–503.
- Holloway, Ralph L., ed. 1974. *Primate Aggression, Territoriality, and Xenophobia*. New York: Academic Press.
- Jolly, Alison. 1972. *The Evolution of Primate Behavior*. New York: Macmillan.
- Kondo, S., et al., eds. 1975. *Contemporary Primatology: Proceedings of the 5th International Congress of Primatology*. Basel: S. Karger.
- Kummer, Hans. 1973. "Dominance versus Possession: An Experiment on Hamadryas Baboons." In Montagna [1973]. Pp. 226–31.
- Kummer, Hans. 1971. *Primate Societies: Group Techniques of Ecological Adaptation*. Chicago: Aldine.
- Kummer, Hans. 1968. *Social Organization of the Hamadryas Baboon*. Chicago: University of Chicago Press.
- Kummer, Hans, and F. Kurt. 1965. "A Comparison of Social Behavior in Captive and Wild Hamadryas Baboons." In *The Baboon in Medical Research*, edited by Harald Vagtborg. Austin: University of Texas Press. Pp. 65–86.
- Ladurie, Emanuel LeRoy. 1978. *Montaillou: The Promised Land of Error*, trans. by Barbara Bray. New York: Braziller.
- van Lawick-Goodall, Jane. 1975. "The Behavior of Chimpanzees." In *Hominisation und Verhalten*, edited by G. Kurth and I. Eibl-Eibesfeld. Stuttgart: Fisher Verlag. Pp. 74–136.
- van Lawick-Goodall, Jane. 1973. "Cultural Elements in a Chimpanzee Community." In Montagna [1973]. Pp. 144–84.
- van Lawick-Goodall, Jane. 1971. *In the Shadow of Man*. New York: Dell.
- van Lawick-Goodall, Jane. 1970. "Tool-Using in Primates and Other Vertebrates." In *Advances in the Study of Behavior*, edited by Daniel S. Lehrman. Vol. 3. New York: Academic Press.
- Lee, Richard B. 1968. "What Hunters Do for a Living, or, How to Make Out on Scarce Resources." In *Man the Hunter*, edited by Richard B. Lee and Irven DeVore. Chicago: Aldine. Pp. 30–49.
- McGrew, W. C., et al., 1970. "New Data on Meat Eating by Wild Chimpanzees." *Current Anthropology* 20 (March): 238–39.
- McGrew, W. C., and C. E. G. Tutin. 1978. "Evidence for a Social Custom in Wild Chimpanzees?" *Man* 13 (June): 234–51.
- McGrew, W. C. 1975. "Patterns of Plant Food Sharing by Wild Chimpanzees." In Kondo [1975]. Pp. 304–309.

- McGrew, W. C. 1977. "Socialization and Object Manipulation of Wild Chimpanzees." In *Primate Bio-Social Development: Biological, Social, and Ecological Determinants*, edited by Suzanne Chevalier-Skolnikoff and Frank E. Poirier. New York: Garland. Pp. 261–87.
- Michael, Richard P., and John H. Crook, eds. 1973. *Comparative Ecology and Behavior of Primates*. London and New York: Academic Press.
- Montagna, William, ed. 1973. *Precultural Primate Behavior: Symposium of the IVth Congress of Primatology*. Vol. 1. Basel: S. Karger.
- Morris, Kathryn, and Jane Goodall. 1977. "Competition for Meat between Chimpanzees and Baboons of the Gombe National Park." *Folia Primatologica* 28 (no. 2): 109–21.
- Nagel, Ueli. 1974. "Variations in Cercopithecoid Aggressive Behavior." In Holloway [1974]. Pp. 159–84.
- Neale, Walter C. 1964. "On Defining 'Labor' and 'Services' for Comparative Studies." *American Anthropologist* 66 (December): 1300–1307.
- Nishida, Toshisada, et al. 1970. "Predatory Behavior among Wild Chimpanzees of the Mahale Mountains." *Primates* 20 (January): 1–20.
- Odum, Eugene P. 1971. *Fundamentals of Ecology*, 3d ed. Philadelphia: W. B. Saunders.
- Okono, T. 1973. "Social Relations in a Chimpanzee Colony." In *Behavioral Regulators in Primates*, edited by C. R. Carpenter. Lewisburg: Bucknell University Press. Pp. 85–107.
- Pitcairn, Thomas K. 1974. "Aggression in Natural Groups of Pongids." In Holloway [1974].
- Plooij, Frans X. 1978. "Tool-Use during Chimpanzees' Bushpig Hunt." *Carnivore* 1 (May): 103–106.
- Pryor, Frederic L. 1977. *The Origins of the Economy: A Comparative Study of Distribution in Primitive and Peasant Economies*. New York: Academic Press.
- Pryor, Frederic L. 1973. *Property and Industrial Organization in Communist and Capitalist Economies*. Bloomington: Indiana University Press.
- Reynolds, Vernon. 1965. *Budongo: An African Forest and Its Chimpanzees*. New York: Natural History Press.
- Reynolds, Vernon, and Frances Reynolds. 1965. "Chimpanzees of the Budongo Forest." In DeVore [1965]. Pp. 368–424.
- Rose, M. D. 1978. "The Roots of Primate Predatory Behavior." *Journal of Human Evolution* 7 (February): 197–87.
- Rumbaugh, Duane M., and Timothy V. Gill. 1973. "The Learning Skills of the Great Apes." *Journal of Human Evolution* 2 (May): 171–79.
- Simpson, M. J. A. 1973. "The Social Grooming of Male Chimpanzees." In Michael and Crook [1973]. Pp. 411–507.
- Strum, S. C. 1976. "Reply." *Science* 191 (23 January): 315–17.
- Strum, S. C. 1975. "Primate Predation: Interim Report on the Development of a Tradition in a Troop of Olive Baboons." *Science* 187 (28 February): 755–57.
- Sugiyama, Yukimaru. 1973. "The Social Structure of Wild Chimpanzees: A Review of Field Studies." In Michael and Crook [1973]. Pp. 376–410.

- Teleki, Geza. 1974. "Chimpanzee Subsistence Technology: Materials and Skills." *Journal of Human Evolution* 3 (November): 575-94.
- Teleki, Geza, et al. 1976. "Demographic Observations (1963-1973) on the Chimpanzees of Gombe National Park, Tanzania." *Journal of Human Evolution* 5 (November): 559-99.
- Teleki, Geza. 1975. "The Evolution of Primate Subsistence Patterns." A paper delivered at the 141st Annual Meeting of the A.A.A.S., 28 January.
- Teleki, Geza. 1973. *The Predatory Behavior of the Wild Chimpanzees*. Lewisburg, Pa.: Bucknell University Press.
- Teleki, Geza. 1977. "Spatial and Temporal Dimensions of Routine Activities Performed by Chimpanzees in Gombe National Park, Tanzania: A Ethological Study of Adaptive Strategy." Ph.D. diss., Pennsylvania State University.
- Teleki, Geza. 1977. "Still More on Predatory Behavior in Non-Human Primates." *Current Anthropology* 18 (no. 1): 107-108.
- Teleki, Geza. 1975. "Primate Subsistence Patterns: Collector-Predators and Gatherer-Hunters." *Journal of Human Evolution* 4 (March): 125-84.
- Thompson, Philip R. 1975. "A Cross-Species Analysis of Carnivore, Primate, and Hominid Behavior." *Journal of Human Evolution* 4 (March): 113-24.
- Torii, M. 1975. "Possession by Non-Human Primates." In Kondo [1974]. Pp. 310-13.
- Washburn, Sherwood L., and Irven DeVore. 1963. "The Social Life of Baboons." In *Primate Social Behavior*, edited by Charles H. Southwick. Princeton, N. J.: Van Nostrand. Pp. 98-111.
- Washburn, Sherwood L., and David L. Hamburg. 1965. "The Study of Primate Behavior." In DeVore [1965]. Pp. 1-19.
- Wilson, Edward O. 1978. *On Human Nature*. Cambridge, Mass.: Harvard University Press.
- Wilson, Edward O. 1975. *Sociobiology: The New Synthesis*. Cambridge, Mass.: Harvard University Press.
- Wolfe, John B. 1936. *Effectiveness of Token-Rewards for Chimpanzees*. Comparative Psychology Monograph 12. Baltimore: Johns Hopkins Press.
- Wrangham, R. W. 1977. "Feeding Behavior of Chimpanzees in Gombe National Park, Tanzania." In Clutton-Brock [1977]. Pp. 504-38.