American Handbook of Psychiatry

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e-Book 2015 International Psychotherapy Institute

From *American Handbook of Psychiatry: Volume 6* edited by Silvano Arieti

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New Evidence on Possible Origins of Human Behavior

The search for information about man's evolutionary history has gradually yielded a wealth of fossil evidence that, together with accumulations of stone tools and detailed mapping of bones and other artifacts found on living sites, has given us an ever-growing understanding of man's physical and cultural evolution. The fossil evidence, however, provides us with few clues as to the social behavior of our earliest known ancestors.

In recent years, an attempt has been made to reconstruct some aspects of prehistoric man's social life by drawing on our growing knowledge of the social behavior of the living primates. Because baboons may live on the savanna in conditions similar to those which nurtured emerging man, these primates have often been selected as a model for the behavior of our remote ancestors. Certainly, baboons and men are both primates and thus share a variety of primate traits, and certainly we can learn much from studying the ways in which a nonhuman primate has adapted to savanna living.

The chimpanzee, however, is a much closer relative of man than the baboon. This is suggested by many lines of research into the biochemistry, physiology, anatomy, and behavior of the chimpanzee. In all these areas there

are striking similarities between the chimpanzee and ourselves. Indeed, in some ways chimpanzees, along with the other African apes, the gorillas, are biologically closer to man than they are to the orangutan—certainly closer than to the baboon. Unless we postulate a remarkable case of parallel evolution in a whole variety of physical and behavioral traits, the African great apes must, at some time, have shared a common ancestor with man. Thus we are suggesting that an understanding of the biology and behavior of the living chimpanzee, while it certainly cannot give us an accurate model for the behavior of early man, may well be the best that is available to us.

We suggest that these biological and behavioral characteristics which can be observed in the chimpanzee today and which show marked similarities to biological and behavioral characteristics of modern man are also likely to have been present both in the primate that served as the common ancestor and in the first true man.

An understanding of chimpanzee biology and behavior highlights those aspects which make man unique as a primate species. After we pinpoint these differences between ourselves and our closest living relative, we can then look for modes of behavior in the chimpanzee that might foreshadow human patterns. Next we can inquire about the environmental conditions in evolution that might, through natural selection, shape these precursors in a direction toward the ultimately human patterns. Clues to the evolutionary

shaping of early man's behavior are relevant to the most fundamental considerations of human nature. A better understanding of the life of early man can lead to a recognition of crucial behavior patterns, which must have been highly adaptive in those times. A significant part of contemporary man's genetic and cultural heritage may lie in a readiness to learn such behavior patterns, some of which may not be appropriate to the problems we face today.

Some Similarities in the Behavior of Man and Chimpanzees

Some of the more striking similarities between the chimpanzee and man are the following: (a) tool-using and tool-making; (b) hunting, cooperation, and food sharing; (c) the length of the period of childhood dependence on the mother; (d) the relationships between a mother and her offspring and between siblings; (e) some aspects of adolescence; and (f) some of the gestures and postures that form the nonverbal communication patterns of man and chimpanzee.

Behaviors described in this section very probably occurred, in a similar (sometimes very similar) form, in the common ancestor of the chimpanzee and man as well as in the earliest true men.

Before describing these behaviors it may be helpful to present a brief outline of the habitat, social structure, and daily behavior patterns of free-

living chimpanzees. We are drawing on data collected during a longitudinal study of the behavior of chimpanzees in the Gombe Stream area in Tanzania, East Africa. This study was started by Jane van Lawick-Goodall in 1960. Since 1965 a growing staff has collected detailed information on many facets of chimpanzee behavior. Hugo van Lawick has developed an extensive record of chimpanzee behavior on 16-mm. film.

Chimpanzees live throughout the equatorial forest belt of west and central Africa, extending eastward to the northwestern forests of Uganda and for a few miles inland from the eastern shores of Lake Tanganyika. The Gombe National Park supports a population that is close to the easternmost limits of the species' range.

The Park comprises a narrow stretch of rugged mountainous country running for some ten miles along the eastern shores of Lake Tanganyika and inland only about three miles to the tops of the peaks of the rift escarpment. The rift is intersected by many steep-sided valleys that support permanent streams. In the valleys, riverine gallery forest is found. Between the valleys, the country is more open, supporting deciduous woodland; and many of the ridges and peaks are grass covered. The area supports a population of between 100 and 150 chimpanzees.

Chimpanzee populations may be loosely divided into communities of

individuals who recognize each other. Within a community, which usually includes about forty individuals, chimpanzees move in small temporary associations, membership of which is frequently changing as individuals or groups of individuals split off to join other associations. These groupings may be all males, females and youngsters, or combinations of different age-sex classes. Some chimpanzees in a community meet only when circumstances, such as a local abundance of food or a female in estrus, throw them together; others meet more often; some show strong bonds of mutual attraction and frequently associate. A mother and her dependent offspring form the one association that may remain stable over a period of years; such a family unit frequently moves about for a while with other associations.

In the wild, chimpanzees probably always lived in male dominated societies though in captivity a female may have the highest social status in a group. Individuals of a community who frequently associate show a fairly well-defined dominance hierarchy; among chimpanzees who meet rarely the relative social status may be less clear. As yet there is little information on relationship between individuals of different communities.

Chimpanzees are omnivorous, feeding mainly on a variety of plant material, especially fruits; but they also consume insects, occasional birds' eggs or fledglings, and sometimes they actively hunt small mammals. They follow no set route, day after day, in their search for food. Within a fairly large

home range (it may cover twenty square miles per year for a male) they are nomadic, sleeping wherever dusk finds them. They typically move on the ground when traveling and spend a considerable portion of each day on the ground. They also spend a good deal of time in the trees both during feeding and at night. They construct quite elaborate nests for sleeping; each individual usually makes a new nest every night except for youngsters of up to five or six years (sometimes older) who share one with their mothers.

In the wild, a female chimpanzee does not give birth until she is about twelve years old, and she has only one infant every four or five years. Life expectancy in the wild is not yet known, but is probably approximately forty years. The longevity record for a captive chimpanzee, a female who was still fertile up to the time of death, is forty-seven years.

Tool-using and Tool-making

For many years the chimpanzee has been known to use objects as tools in captivity and, as far back as 1843, there was a report of a chimpanzee using a tool in the wild. It is, however, only within the past decade that we have begun to learn something of the variety and frequency of chimpanzee tool-using and tool-making behavior in the natural habitat.

Tool-using in animals has been of much interest to students of human evolution because, for a long period, man was commonly referred to as *"the*

tool-using animal." In fact, a variety of animals do use objects as tools, but it should be emphasized that tool-using ability on its own does not indicate any special kind of intelligence. The Galapagos woodpecker finch uses a cactus spine to probe insects from crevices in the bark. This is fascinating behavior, but it does not make this bird more intelligent than the ordinary woodpecker, which uses its long beak and tongue for the same purpose. The Galapagos finch uses a behavioral adaptation while the woodpecker uses a morphological one. To further this argument we need only point out that there are some invertebrates that quite clearly use objects as tools. The ant lion who hurls grains of sand at prospective prey, causing it to fall into its pit in the ground, is a good example.

The point at which tool-using and tool-making in a nonhuman animal acquire significance, when viewed in relation to the evolution of tool-using behavior in man is, surely, when an animal can adapt its ability to manipulate objects for a wide variety of purposes and, in particular, when it can use an object spontaneously to solve a novel problem. Chimpanzees have shown themselves capable of using a wider variety of objects as tools for a wider variety of purposes than any other living creature except for man himself (Good all, 1970).

Research at Gombe has revealed that this one community of chimpanzees uses four different kinds of objects—grasses, sticks, leaves, and

rocks—in a wide variety of different contexts during feeding, investigating, body care, and aggressive interactions. Moreover, if the object is not suitable for the specific purpose for which it is to be used, the chimpanzees will modify it accordingly. While they do not show any kind of sophisticated tool-making behavior, they certainly show the crude beginnings.

They use stems and grasses when feeding on termites. The tool is pushed down into the termite nest and then withdrawn, covered by termites clinging on with their mandibles. The chimpanzees pick these off with their lips. If they choose a leafy twig, they strip the leaves off prior to using the twig as a tool. Similarly, a wide blade of grass may be trimmed to size. The chimpanzees use larger sticks to push into ants' nests, and sometimes use a short stick to enlarge the opening to an underground bees' nest. In an earlier time when boxes with bananas in them were made available in a special area, the chimpanzees often used sticks to pry open the boxes. In these different situations, stick selection and modification are varied in accordance with the requirements of the situation.

Quite often during feeding a grass stem or twig may also be used as an investigation probe. For instance, a chimpanzee may push such a tool into a hole in a piece of dead wood and then withdraw it and intently sniff the end. After this he either leaves the wood or tears it apart; this usually reveals the larvae of some insect which is then eaten. Before working at a termite hole, a

chimpanzee will commonly push the tool down and sniff the end, after which he either works the hole or moves to try a new one. Sticks are used in a similar way to investigate objects that the chimpanzees are frightened to touch: one individual carefully touched a dead python with the end of a long stick and then sniffed the tip. Another, after his mother had repeatedly pushed his hand away, used a short stick to touch his newborn sibling.

These chimpanzees use leaves as a kind of sponge to sop up water that has collected in the hollow of a tree trunk and which they cannot reach with their lips. And this provides us with another example of crude tool-making. For the leaves are always briefly chewed before use to increase their absorbency. One individual used a similar sponge to clean out the last fragments of brain from inside the skull of a baboon. The chimpanzees also use leaves to wipe dirt from their bodies.

Individual tool-using performances (i.e., patterns that have been observed on one occasion only) were as follows: (1) an adult female used a short twig to pick at something stuck between her teeth; (2) an infant picked inside his nostril with a twig; (3) an adult male lined his hand with leaves before defecating into this "cup." He was then able to pick out small pieces of undigested flesh of a bushbuck he had fed on earlier without soiling his hand; (4) an adult male used a stick to hit a banana from a human hand when he was too apprehensive to reach for it with his own hand; and (5) a juvenile

killed a skink (a kind of lizard) and then laid leaves over it before stamping on it with his foot.

In addition to the use of objects as tools in feeding, self-care, and investigation, the chimpanzees at Gombe also use objects as weapons in aggressive contexts. Rocks and sometimes sticks may be hurled, often with considerable accuracy, during aggressive encounters with other animals. When baboons competed with chimpanzees for bananas at an artificial feeding area, the apes frequently threw rocks. Over a three-year period, more and more individuals began to throw objects as missiles, and they tended to select rocks that were larger and thus potentially more dangerous than the ones they had used initially. No baboon was observed to use any object as a missile during these encounters. Rocks and stones may also be thrown at conspecifics and humans. Sticks or palm fronds are sometimes brandished during aggressive displays and occasionally used as clubs to hit an opponent. One infant used a stick as a club to hit an insect on the ground.

In captivity chimpanzees often use objects quite spontaneously as tools. Wolfgang Kohler studied one group in which the individuals used sticks to pry open box lids and also to dig up roots to eat. They wiped themselves with leaves or straw, scratched themselves with stones, and pushed straws into columns of ants to feed on them. They also used sticks and stones as weapons. Sometimes they used bread to lure chickens close to their cage where they

would suddenly prod the birds with sharp sticks, apparently in play.

In another group poles were used as ladders to enable the chimpanzees to climb past electric wiring into trees and escape from the enclosure. In the same group, several individuals used twigs or other material to remove loose deciduous teeth: one of them actually extracted a tooth of a companion with a short piece of stick. Another captive individual was observed to push small slivers of sharp stick under his fingernail, apparently in order to try to relieve the pain caused by a very swollen fingertip. He used the slivers only after repeatedly sucking and biting at the affected area with his teeth.

In laboratories many experiments have been designed to investigate the "tool-making" ability of chimpanzees. This work has shown that a chimpanzee can pile as many as five boxes, one on top of the other, to reach hanging food; that he can fit as many as three tubes together to make a tool long enough to reach food that has been placed outside his cage; and that he can uncoil a length of wire for the same purpose. So far, no chimpanzee has been able to use one tool to make another. However, to our knowledge little experimental work has been attempted in this field. In one series of tests a chimpanzee was repeatedly shown how to use a hand ax to break off a splinter of wood for use as a tool. However, she was unable to do this and did not even try to manipulate the ax to achieve the desired purpose. Instead she continued to try to break the wood with her hands and teeth—a method that had been

successful in previous experiments with softer wood. Before drawing conclusions from this experiment, it is important to realize that chimpanzee intelligence varies considerably from one individual to another. It is quite possible that further tests along similar lines, using different chimpanzees, might yield very different results. An orangutan did learn how to use a stone to chip a flake from a core: he then used the flake to cut nylon string to obtain a food reward.

We think it would be particularly interesting for one chimpanzee to act as a model for another chimpanzee under experimental conditions in which: (a) the model made congenial movements (i.e., easy for a chimpanzee) in making (b) a relatively complex tool that then provided access to (c) a highly valued reward (d) under circumstances in which the reward could be obtained in no other way. Conditions of this sort would tend to elicit the full tool-making potentialities of chimpanzees, taking into account individual differences.

We know that observational learning and imitation play a highly significant role in the tool-using cultures of our own species. Can we say the same of the chimpanzee? The answer is almost certainly in the affirmative. For, while the ability to manipulate objects in a manner that enables them to be used as tools is undoubtedly genetically coded in the chimpanzee, there is increasing evidence that the different tool-using patterns of different

chimpanzees are passed from one generation to another by observation, imitation, and practice.

Infant chimpanzees, during their long period of dependency on their mothers, have much opportunity for watching tool use in their elders, particularly during termite fishing. In this context an infant of less than one year sometimes watches his mother intently for a few minutes, and he often picks up discarded tools and plays with them. During the following year's termiting season, he watches adult patterns more intently and during his play with grass and twigs he may "prepare" them for use as tools, stripping leaves off twigs, and so on. He may also make clumsy attempts to push tools into the nest—frequently where there is no hole. Initially, he tends to choose pieces of grass that are much too short: subsequently he uses longer tools, but ones that are too pliable. Gradually, during the next two years, his tool-using attempts mature. His movements become less awkward, and he begins to select material more suitable for use as a tool. This improvement is partly due to the maturation of the necessary motor patterns, but, almost certainly, it is also due to experience gained during practice. By the age of about five or six, the youngster is usually a skilled termite fisher.

It is not only in infancy that observational learning may play a role in the development of tool-using behavior. We mentioned earlier that at the special feeding area chimpanzees sometimes used sticks to try to pry open

boxes containing bananas. This practice was first seen in three juveniles and for each of them it appeared to be an individual attempt to solve the problem. Subsequently, more and more individuals of the community began to use sticks, and it certainly appeared that they were gaining experience by watching the behavior of the others. However, until one adult female tried to open a box with a stick, on the *first* occasion that she dared leave the bushes surrounding the feeding area and venture into the open, proof was lacking. Since it is very unlikely that a chimpanzee with no prior experience of boxes would automatically use a stick to pry open a box, we may assume that she had learned the behavior by watching her companions from the bushes. The fact that she had been seen observing this behavior on previous occasions reinforces this assumption.

In captive colonies, it is an established fact that novel patterns may spread from one individual to another through observation and imitation. At the Yerkes Laboratory, for example, it was only necessary to teach one adult chimpanzee how to use a water faucet. All other members of the colony learned the pattern by observing him and each other. In the colony mentioned earlier the pattern of poking at the teeth with twigs was an innovation of one adolescent female, and it was soon transmitted to other individuals through observational learning. Similarly, the use of poles as ladders was “invented” by one of these chimpanzees and subsequently imitated by the others.

If tool-using behavior in the chimpanzee does represent a kind of primitive culture (where culture is defined as the passing on of information from one generation to the next by learning) then we would expect to find different tool-using patterns in different parts of the chimpanzee's range. As yet there are only two indications that this is so: (a) in two areas in west and central Africa, chimpanzees have been observed using rocks as hammers to open hard-shelled fruit or kernels and (b) in Uganda, chimpanzees have been seen using leafy twigs as fly whisks. At Gombe no chimpanzee has been seen to use a stone for any food-getting purpose although one infant, once, pounded at an insect on the ground with a stone. Nor have these chimpanzees been seen using twigs as fly whisks.

However, other tool-using patterns appear to be widespread throughout the range of the chimpanzee: termite-fishing behavior has been reported from another area in Tanzania, in Rio Muni, and in one individual of a group of wild-born, semi-captive chimpanzees in the Gambia. The use of sticks or twigs during honey feeding has been seen in Western Tanzania and the Cameroons as well as at Gombe. The use of leaves for a drinking sponge has been observed also in one of the chimpanzees in the Gambia group. The fact that some chimpanzee tool-using traditions are widespread should not be surprising since some identical stone-tool cultures of early man have been excavated in widely separated areas of the globe.

It seems sensible to suppose that early man used similar perishable tools (sticks, stems, and leaves) prior to his known use of stone implements. Indeed, the Bushmen of the Kalahari and one tribe of South American Indians use the leaf sponge to this day; and almost anyone will use a stick or some other long shaped object to investigate a frightening object—to find out, for instance, whether a snake or a spider is alive or dead. And it is not only chimpanzees who hurl any object at hand in moments of rage.

Hunting, Cooperation and Food Sharing

Until the last decade, man was the only living primate known to hunt in organized groups, nor was it even suspected that hunting and meat eating might occur frequently in a nonhuman primate. Now, however, it is known that wild chimpanzees may hunt quite large mammals for food, sometimes in a quite organized manner. This has been observed at Gombe, in other areas of Tanzania, in Uganda, and in a wild-born semi-captive group in the Gambia.

The prey most frequently selected by the chimpanzees at Gombe is other primates— adult and young monkeys of three different species and infant and juvenile baboons. These chimpanzees also hunt young bush-bucks and young bush pigs.[2]

Meat-eating behavior often occurs in clusters. Possibly an “accidental” kill (such as when a chimpanzee comes upon an unprotected infant prey)

triggers off a “craving” for meat. Then a series of kills, together with a number of unsuccessful hunts, may follow in relatively quick succession. Such a meat-eating phase may stretch over a number of weeks and then either because the craving is assuaged, or, perhaps because the chimpanzees have a succession of failures, the cycle passes and the apes resume their usual plant and insect diet for the next few months. Up to twenty-two instances of meat eating have been recorded in one year for a community of about thirty-five to forty individuals; but in some years few predations occur. As yet, little is known of the factors governing the initiating causes, frequency, and duration of hunting periods.

Nearly all the hunting episodes observed during the past eleven years were initiated by males, but on one occasion two females were each observed to catch a baby bush pig.

Sometimes one chimpanzee chases after and seizes a small animal. The hunt is then an individual affair. At other times, however, a group of males may surround a potential victim, such as a young baboon temporarily isolated from its troop. This has been observed on five occasions. Although the eating of meat has been observed on many occasions, the actual hunt has been observed much less frequently. In each of the five instances of observed group hunting, a single chimpanzee (twice he was an adolescent male) climbed very slowly and silently up the tree toward the intended victim. The

other males stationed themselves at the base of that tree and other trees that could be used as escape routes. Three times the victim managed to escape. On the two occasions when it did not, the waiting members of the hunting group then raced up to share in the meat.

Cooperation can also be observed when a group threatens a frightening object or when two or more chimpanzees challenge a chimpanzee who may be socially superior to most or all of them individually. In these instances, however, each individual of the group is playing a more or less similar role: each one is concerned with intimidating a potential predator or subduing an aggressive superior. The actual gestures used by the different individuals may vary, but the overall patterns are similar.

In the group-hunting incidents described above, it seems that the cooperative behavior is on a slightly different level since two quite distinct activities or roles are enacted: one chimpanzee is responsible for stalking and attempting to seize the prey, while the others are responsible for trying to prevent its escape. If each individual were solely concerned with *his own* chances of making the capture, one would expect a frenzied rush in which each chimpanzee tried to be the first one up the tree. But no such thing happens. Indeed, on one occasion, a group of adult males waited silently on the ground for over two minutes, staring intently up at a young male slowly chasing a juvenile baboon back and forth from the crown of one palm tree to

another. Not one of the waiting males left his position on the ground in order to try to get closer to the prospective feast. Only when the victim finally took a wild leap to the ground and the direction of its flight became apparent, did the other chimpanzees run to converge on the baboon. We certainly cannot rule out the possibility that each of the males on the ground considered that his own chances of making the capture were just as good as those of the young male up in the tree. Whatever the motivations of such a group of individual hunters may be, the result is an effective demonstration of quite sophisticated cooperation. Detailed, sequential observation of complex cooperation has been made at Gombe in contexts of dominance interaction as well as hunting.

Meat appears to be a much favored food: intense excitement is shown by all chimpanzees present at the time of a kill. They usually scream loudly and embrace or touch one another. The commotion is likely to attract other chimpanzees within earshot to the scene. In all cases when a kill was made and when other chimpanzees were present during or subsequent to the event, hunting resulted in food sharing. Prior to the observations at Gombe, no nonhuman primate had been reported to share food in the wild with the occasional exception of mothers with their infants.

After a kill at Gombe other individuals gather around the chimpanzee (or chimpanzees) in possession of the carcass or portions thereof and show a variety of begging gestures. They may reach out to touch the carcass, while

looking at the male in possession as though seeking his permission to take some food. They may reach out to touch his mouth. Or they may hold their hand toward him, palm up, in the common begging gesture of man. The response of the feeding male varies with his personality, the amount of meat available, the amount he has already consumed, and his relationship with the begging individual. Sometimes a chimpanzee is permitted to feed from the carcass along with the male in possession; sometimes it is permitted to detach a piece of flesh; less often it is actually *given* a share of the meat that has been detached, the male in possession placing the meat in the outstretched hand of the begging chimpanzee. During the eating of meat, the chimpanzee invariably puts a handful of leaves in with each mouthful of meat, and one of the most common forms of sharing occurs when an individual chewing such a wad is finally persuaded to spit it into the waiting hand of another.

There are, of course, many occasions when a chimpanzee in possession of a carcass responds unfavorably to begging, either by moving or turning away or by mildly threatening the begging individual. If fighting occurs during meat eating, it is usually when a male without a share of the carcass chases or attacks an individual subordinate to himself who is also without meat—an example of what is commonly referred to as redirected aggression.

Food sharing among adults does occur in some other contexts. We have

repeatedly seen an old mother sharing bananas, another highly valued food, with her adolescent son. But it is during meat eating that food sharing is seen most frequently and most dramatically. Once, for instance, an adult and very high-ranking male actually tore in half the body of an infant baboon he had caught and handed one piece to a low-ranking adult male who had been begging and having tantrums for the previous ten minutes. An average-sized carcass, such as that of a young baboon, may well be shared by fifteen individuals, although the portions are by no means equal. The older males and the older and more persistent females or those in estrus are likely to get the largest pieces.

Period of Infant and Juvenile Dependency

Possibly one of the most striking findings to emerge from the longitudinal study at Gombe is the length of the period of infant and juvenile dependence on the mother. The infant is totally dependent on his mother for food, transport, and protection during the first six months or so. At about six months the infant takes its first tottering step. But steady locomotion does not occur until the third year and riding on its mother's back continues to be the main manner of getting from place to place until the fourth year.

The first minute amounts of solid foods are ingested at about six months of age, but milk continues to be the principal source of food for at least two

years and possibly longer. Youngsters usually complete weaning during their fifth or sixth year; the youngest to be weaned, so far, was four and a half years. One male infant, early in his seventh year, is being finally weaned at the time of this writing. This weaning roughly coincides with the eruption of permanent dentition as with some human groups, e.g., Eskimos. (Schultz has argued that a higher percentage of well-worn deciduous teeth in early human children as compared with chimpanzee children indicates that early man had a longer childhood. But perhaps extra wear from eating roots and other rough foods might account for the difference.) The weaning process may continue for over a year, the mother gradually rejecting her child more and more frequently but usually giving access to the nipple if it persists. Ultimately weaning appears to occur as a result of physiological changes in the mother, but these are not clear-cut since lactation may continue during pregnancy in some females.

Youngsters may continue to sleep with their mothers after being weaned. Usually they start sleeping in their own nests at night during the sixth or seventh year; if they are not already independent at night, they usually become so at the birth of a new sibling. One youngster continued to share his mother's nest at night until her death when he was eight and a half years old.

During its sixth or seventh year, a juvenile sometimes accidentally

becomes separated from its mother. This usually results in obvious distress on the part of the child and sometimes the mother which may persist until the two meet again. During his seventh or eighth year, the male juvenile may begin to move about in a group away from his mother for a few hours or even days. But until he is at least nine years old, he does not spend long periods away from her except accidentally. The female offspring is likely to remain almost continuously with her mother for an even longer time.

As in man, the long period of dependency in the chimpanzee is adaptive in relation to social learning. When the youngster is traveling with and protected by its mother it has much opportunity for observation and learning. We have already presented evidence for the role played by observation, imitation, and practice in the acquisition of tool-using behaviors. Similarly the young chimpanzee frequently watches and subsequently imitates and practices a variety of other behaviors such as nest making, some kinds of feeding patterns as well as a variety of social patterns, notably maternal behavior for females and sexual behavior for males.

Indeed, we have a clear-cut example of the role played by observational learning in maternal behavior. A juvenile female, who spent long periods close to her mother and newborn sibling, carefully watching everything that went on, was one day offered a toy chimpanzee. She carried it pressed in the ventral position in the same way that her sibling was transported at that time.

A month later, when her sibling had just commenced to ride on his mother's back, she was again given the toy. This time she immediately pushed it up onto her back when she walked off. This same female has now had her first infant and it is significant that several of her maternal practices show striking similarities to those of her mother.

Another aspect that should be considered here is that the long period of dependence prolongs the time when play is a frequent activity of the infant and juvenile chimpanzee. While play is a controversial category of behavior, both as to definition and function, there can be little doubt that the experience gained during locomotor and social play is valuable to the growing youngster. Compared to the playful activities of primates such as baboons, young chimpanzees exhibit an extremely rich variety of play patterns, both during social and solitary play. Once we observed how a novel mannerism, incorporated by one infant into her social play, spread to the other youngsters of her community in a few weeks. In this case, it was merely a nonfunctional facial expression (she sucked in her cheeks) and it was eventually dropped from the repertoire. But it remains a possibility that behaviors "invented" during play might sometimes lead to a new tradition or culture in the group.

It is apparent that just as observation, imitation and practice play a vital role in the development of human behavior, so too these processes are important in the development of chimpanzee behavior, as well as in that of

other nonhuman species such as Japanese macaques.

Relationships within the Family

A chimpanzee "family" comprises a mother, her offspring, and any offspring of her daughters. This differs from the human family unit in that no father is included. In the wild, it has so far not been possible to know which chimpanzee has sired which infant. Even on those occasions when a female was presumed to have been with one male only at the time of conception, such a pair has never been followed long enough without interruption to obtain sure evidence of paternity. However, new data on this subject is becoming available. In any event, the father plays no role in family life subsequent to the time of conception: the tasks of child raising lie solely with the mother, sometimes assisted by an older daughter.

An important finding of the long-term study at Gombe has been the realization of the strength and duration of the affectionate ties between a mother and her offspring and between siblings. Indeed, in most primate species, there is initially a close, affectionate relationship between a mother and her infant. But in those species where long-term studies have been carried out, these bonds have been found to be more persistent than was formerly supposed, particularly between mothers and their daughters. This applies to rhesus monkeys on Cayo Santiago, Japanese monkeys, and olive

baboons.

In the chimpanzee, however, the period of juvenile dependence on the mother is extremely long. It is characterized by a variety of affectionate behaviors and by a marked sparsity of pain-eliciting stimuli as compared with other mother-offspring relationships in primates such as baboons and macaques. Mother chimpanzees spend much time in grooming and playing with their youngsters and very seldom administer physical punishment. When they do, it is often followed by an embrace or some other reassuring gesture in response to the whimpering or screaming of the child.

The extent to which the young chimpanzee depends upon his mother is strikingly revealed when she dies. A three year old, who was probably still fairly dependent on maternal milk, survived her mother by some two and a half months. During this time she showed patterns similar to human depression—huddling, spending long periods in almost complete inactivity, almost total suppression of playful activity, and loss of appetite. She became increasingly lethargic. Finally she disappeared and was presumed dead. Two youngsters lost their mothers when they were between four and five years of age, and although both were “adopted” by elder sisters, they too showed signs of lethargy and abnormal behavior. One of them made a gradual recovery, and she behaved in a manner comparable to her peers a year after her mother’s death. The other became increasingly abnormal and emaciated, and he finally

died about one and a half years after losing his mother.

One juvenile male of about seven or eight years showed few signs of depression when he lost his mother and infant sibling. He was, however, fairly independent by this time and had quite frequently traveled on his own. An eight and a half year old who was still sharing his mother's nest at night and traveling with her constantly only survived her death by three weeks. He showed signs of severe depression by the second day and made only a few journeys away from the area where he last saw her body. He huddled, stopped playing, stopped eating, and was largely unresponsive to environmental stimulation. While in this condition, he developed gastroenteritis which probably contributed to his death twenty-five days after the death of his mother.

Even when young chimpanzees have attained some measure of independence and begun to move around for days or weeks with other individuals, they still spend much time in between such ventures associating with their mothers. A late adolescent male who was spending most of his time traveling apart from his mother began once more to move about with her frequently after cutting his foot badly. Another son of the same female, an adult male of some eighteen years, also traveled around constantly with her, away from other chimpanzees, after spraining his wrist in a status conflict. He only left her when he was fully recovered. This female was frequently

accompanied by her three fully mature offspring until the time of her death, and the two other mothers known to have adult offspring were also often accompanied by them until death.

Mother chimpanzees not only actively protect their offspring during infancy, in common with mothers of all mammalian and avian species, but will usually try to protect their older offspring also. There is considerable variation in the extent to which individual mothers will attempt to assist their juvenile and adolescent daughters, but so far all mothers have at least hurried to the scene when their juvenile or adolescent sons were threatened or attacked by other chimpanzees. One mother rushed up when her young adult son was screaming and retreating from an older but rather low-ranking male. When she appeared, her son turned on his aggressor and together mother and son chased him away. This same female was observed to run half a mile, fast, when she heard her adult son (probably close to eighteen years) screaming during a serious attack. When she arrived, the action was over but her presence seemed to calm her son, who gradually stopped screaming. Similar behavior has been observed in rhesus monkeys.

Adolescent sons have been observed to rush to their mother's defense in social encounters, and sometimes an entire family will present such a united front in the face of aggression that it is able to intimidate a male who would easily be able to dominate each of the members individually.

Of interest is the fact that we have never yet observed a physically mature male try to mate with his mother. Our sample size is too small for conclusions to be drawn about this, since it only involves two mothers, one with two adult sons and the other with one. However, during four days of estrus, the mother with two adult sons was mated by every mature male in her group *except* her two sons. Several adolescent males of lower rank than the two sons were observed mating with the female, so it cannot be argued that the sons were of too low a social status to mate with a popular female. There are indications that mother-son matings are infrequent in Japanese macaques and rhesus macaques. In these macaque species, the sons usually transfer out of their natal troops shortly after puberty, so there is less opportunity for sexual interactions with their mothers.

Mating does occur between a brother and his sister, but it is extremely rare. One female, when first she came into estrus, repeatedly ran off screaming on the few occasions when her two adult brothers tried to mate with her. Eventually she permitted them to copulate with her, but subsequently they have been observed to approach her sexually only a few times. Another brother-sister pair was seen mating only once during the two years when she had periods of estrus prior to conception. Another female who has been receptive to adult males for two years has not yet been seen having sexual relations with her elder brother.

The relationship between siblings is sometimes very strong and enduring. Juvenile and adolescent female chimpanzees may spend a great deal of time in watching, grooming, playing with, and carrying around their infant siblings, although this is not always the case. Some juvenile and even adolescent males may also pay much attention to their small siblings. On three occasions when mothers died their orphaned infants were adopted by older siblings, and this was the case even when the older sibling was a juvenile male.

Records at Gombe to date indicate that bonds between siblings of the same sex are likely to be stronger than those between brothers and sisters. Analysis of some of the recent data revealed that each individual of five adolescent and adult sibling pairs spent a greater percentage of observed time in association with a sibling than with any other chimpanzee of the same sex and similar age to that sibling. It also showed that brothers associated more with each other than with *any* other individual, at least during one year.

To date we have not been able to follow the development of a relationship between older sisters since the only known pair are both still traveling for most of the time with their mother.

At times a male may back up his brother during an aggressive social encounter. We have not yet seen mutual assistance between brothers and

sisters. However, after a stressful incident an adolescent female hurried to sit close to her elder brother and this, in itself, seemed to have an immediate calming effect upon her. A juvenile female once ran to embrace her elder sister who was screaming and upset after being mated.

It is not only in chimpanzees that sibling bonds between males are known to extend beyond the infant and juvenile stage. A number of close associations between male siblings outside the natal group (that is, after they have transferred to another troop) have been reported among the rhesus on Cayo Santiago. Indeed, at the time of his transfer, a young male is likely to join the group to which one or more of his brothers has already transferred.

The above facts suggest that, whatever the precise structure of the family unit in our earliest ancestors, and whatever the role of the male may have been, it seems reasonable to assume that between mothers and their children and between siblings there were affectionate bonds of long duration, probably for the life span of the individuals concerned in many cases. If sufficient, reliable data can be gathered to show that incestuous relationships between mothers and sons in chimpanzee society do not occur, it will indicate that a similar inhibition was in operation among our stone age ancestors.

Adolescence

The period of adolescence in the chimpanzee commences at puberty

(approximately seven to ten years of age) and ends when the individual reaches social maturity (about twelve or thirteen years of age in the female and fifteen or sixteen in the male). Adolescence is very often considered a culturally determined period unique to man. We shall attempt to show that, as in man, adolescence is an important stage in the life cycle of the chimpanzee, both biologically and psychologically.

It appears that this period is particularly difficult for the male chimpanzee. During puberty he has a growth spurt; he becomes more and more independent of his mother; and he is increasingly able to dominate females who, a short while previously, were able to subdue him with ease. On the other hand, he must behave with increasing caution in order to avoid arousing the aggression of adult males. One of the most interesting aspects of adolescence in the male chimpanzee is his ambivalent attitude to high-ranking mature males. On the one hand, he becomes increasingly fearful in their presence, often flinching at any sudden movement they make whether or not it was directed toward him. On the other hand, he increasingly seeks their company. When he first begins to travel with other groups, away from his mother, it is frequently with a group of adult males that he chooses to associate.

For the most part the early adolescent male occupies a peripheral position in a group of males, often watching them intently but seldom

entering into their activities. For example, with regard to sex his behavior seems to be inhibited by the proximity of highly dominant males. Adolescent males certainly do mate, but seldom with a sexually popular female when there are mature males nearby.

All this suggests that the adolescent male, particularly during early adolescence, goes through a period of gradually changing relationships with many of the individuals of his community. It may well be that his relationship with his mother, which remains relatively constant, is the most stabilizing factor. Often, after associating for a while with males, and particularly when there have been frustrations involved (such as not being able to mate with a female in estrus) he returns to travel about with his mother for a while. Sometimes he may wander off completely on his own for some hours in the forest—e.g., after a thrashing by a dominant male.

During the last years of adolescence, the growing chimpanzee gradually begins to join in activities with the mature males; and he begins to challenge the status of the lower-ranking ones among them. Intense conflicts tend to occur at such times. Over a period of many months, or even several years, he gradually takes his place in the hierarchy of mature males of his community.

For the female chimpanzee, the period of adolescence is less demanding, and her relationship with other members of her community does not change

markedly except during her periods of sexual receptivity. It is unnecessary for the female to leave her family group in order to learn her future role as a mother, and she typically associates with her mother for a more extended period than does the male. Most young adolescent females spend considerable time playing with, grooming, and carrying around an infant sibling or an infant of a nonrelated female.

For some females, the most stressful time of adolescence occurs when she has her first true estrus—that is, the first sexual swelling when she becomes attractive to adult males. Prior to this she has shown smaller swellings that attract the attention of infant males who are sexually precocious and start "mating" before they are one year old; toward the end of this phase she attracts juvenile males and the younger adolescents. Females show much variation in their initial responses to the sexual advances of mature males. Some are extremely fearful and, at least for the first few days, continually try to run from and avoid their suitors; others take such approaches as a matter of course.

In the female chimpanzee, there is a period of adolescent sterility. In wild chimpanzees, the duration of this period ranges from one to three years.

In most nonhuman primates, exchange of genes between groups seems to occur when males from neighboring ranges change groups. This has been

observed in gorillas, rhesus macaques, baboons, and it may occasionally occur in chimpanzees as well. However, we have also recorded a number of instances when young sexually mature female chimpanzees left their home communities during periods of sexual receptivity and mixed with and mated with males of neighboring communities. In at least two cases, "stranger" females have been gradually integrated into the host community and finally abandoned their natal groups.

This may have significance for the understanding of the evolution of intergroup marriages in man. In many human cultures, it is the female who leaves her home and moves into new surroundings, often traveling miles to live with comparative strangers. Sometimes she must adopt a new culture also. In principle, such a major transition might have been facilitated by the evolution of love in the line leading to man, since love can overcome the concerns of strangeness. But most marriages in many cultures have traditionally been based not on love but on arrangements made either by the parents of the couple or by society. This discovery regarding chimpanzee adolescent female behavior, differing as it does from other nonhuman primates, raises questions about the evolution of human mating systems. More information is needed before we can adequately understand this behavior, but it does suggest that similar female restlessness may have been in operation in early man, may have contributed to the exchange of genes between groups, aided young women in coping with the stressful experience

of being “given” to the son of a family in another group, or generally helped women through the difficulty of leaving what is familiar and going to what is largely unfamiliar.

Adolescence, in the chimpanzee as in the human, may be viewed as an extension of the learning period, a period when some of the skills and behaviors learned during childhood can be put to use in the adult context so that the developing individual will be fully prepared to handle the tasks of social maturity. It seems likely that the adolescent period of early man was more like that of the chimpanzee than the adolescent period of any human society after the advent of complex cultures.

Nonverbal Communication

Some of the most striking similarities in the behavior of chimpanzee and man are to be found in the gestures and posture of nonverbal communication. Thus chimpanzees may bow, kiss, hold hands, touch and pat each other, embrace, raise their arms in the air, bite, punch, kick, scratch each other, pull out each other’s hair, and tickle. It is not only that some of these movements look remarkably similar to those of man, but also the behavioral contexts likely to elicit these patterns are similar in the two species.

When an adult chimpanzee is suddenly apprehensive or frightened, he may reach out to touch or even embrace another chimpanzee who happens to

be nearby. Once two adult males were suddenly confronted with their mirror images: they responded with a variety of contact-seeking patterns, touching and patting each other, holding hands, embracing. In such a context, a high-ranking adult male may even embrace an infant or juvenile. Kortlandt and colleagues have filmed the responses of a wild chimpanzee group upon exposure to a stuffed leopard. One of the principal reactions was an intense outburst of mutual embracing, including adult males. It is probable that the quick embrace a mother invariably bestows upon her infant if it utters a sound of fright may serve a mutually reassuring function, calming the fear of the infant and also the discomfort aroused in the mother by the distress signal of her child.

Humans, of course, show similar *contact-seeking behavior in stressful situations,* children and adults alike. Man carries his desire for contact in stress a step further and may caress or even embrace a pet when upset. In the human species, sudden anxiety often elicits self-contact patterns such as wringing the hands or clasping a hand to the breast or mouth. We have observed one wild chimpanzee who frequently clasps his genitals when suddenly fearful. Also, self-grooming is common in anxious chimpanzees.

Captive chimpanzees who have been raised without mothers, or who were separated from them at an early age, show self-contact patterns in moments of stress, mainly clasping themselves. Isolation-reared rhesus

monkeys will actually bite themselves when suddenly alarmed.

The comfort adult chimpanzees and humans alike may derive from close physical contact with another individual must result from the years of infancy when, for so long, the embrace of the mother or contact with her body (or that of a mother substitute) serves to calm the anxieties of ape and human infants. As the child becomes increasingly independent of his mother he may, when suddenly frightened, seek contact with another individual—a temporary mother substitute—if his mother is not close by. Even an adolescent chimpanzee will seek contact with his mother, rather than another individual, if she is available. One adolescent male, after being threatened by a high-ranking male, hurried, whimpering, past several other chimpanzees to reach out toward his mother and hold the hand she extended.

When two or more chimpanzees become suddenly excited—if, for instance, they are confronted by a large pile of favored food— they often exhibit an outburst of contact-seeking behavior with their companions. Three or even four adults may pat each other, embrace, hold hands, press their mouths against one another and utter loud screams for several minutes before calming down sufficiently to start feeding.

This kind of behavior is similar to that shown by a human child, who, when told of a special treat, may fling his arms ecstatically around the bearer

of the good news and squeal with delight. Similar adult responses in a variety of cultures are common experiences, though the intensity of expression is usually less exuberant.

Some chimpanzees consistently try to ingratiate themselves with more dominant animals. One female of our group seldom missed the opportunity of approaching an adult male who was passing anywhere near. Then, uttering submissive grunts, she would lay her hand on his head or back. Presumably, the sight of a high-ranking male makes such individuals uneasy: to calm themselves they approach and seek contact. There may be a similarity here to the uneasy human, who, during conversation, repeatedly reaches out to touch the person with whom he is talking.

A brief comment should be made here with regard to the human smile. It seems that we smile in two different contexts. We smile when we are pleased, happy or amused; and we smile also when we are uneasy and apprehensive. During a tense interview, a person may sit on the edge of his chair, clasp his hands, and smile. Indeed, he may smile at almost everything that is said, even when the content is unsatisfactory for him. This kind of tense, apprehensive smiling in man may be similar to the “grin” of the fearful or apprehensive chimpanzee in which the corners of the lips are drawn back and the lips slightly parted to expose the teeth.

After a chimpanzee has been severely threatened or attacked, particularly if the victim is a youngster, his need for physical contact is often dramatically illustrated. An adolescent may approach his aggressor after being attacked, still screaming, and obviously fearful. When he finally reaches the other, he will crouch, making gestures of appeasement or submission. In response, the aggressor will usually reach out and touch or pat the subordinate. He may continue patting gently until the youngster gradually stops screaming and whimpering. We have seen clear examples of conflict situations as adolescents approach an aggressor, so fearful that they keep turning away as though to flee, yet so much in need of a reassuring contact that they turn back and approach. In this manner they slowly come nearer and nearer the aggressor in a series of circles as the desire to flee is overcome by the desire for contact, and vice versa. Youngsters have actually flown into violent tantrums, beating the ground and screaming, when the dominant chimpanzee did not respond with an appropriate contact behavior to their submissive gestures.

A very similar pattern is observed when a young human child who has been punished proceeds to follow the disciplinarian, crying, often clutching at legs or clothing, until he is picked up, petted, and forgiven. After a family dispute has been resolved, the people concerned often “make it up” with a kiss, embrace, or some other form of contact behavior. And the clasping of hands to denote mutual forgiveness and the renewal of friendly relations

after a quarrel is common in many cultures.

However, this whole sequence of events—aggression, contact-seeking, and reassurance—is far from easy to understand in chimpanzees. Why should the dominant chimpanzee respond with a comforting gesture? When we think in human terms, this is the kind of action that we tend to regard as an expression of apology or sympathy or kindness. Does the dominant chimpanzee therefore show the beginnings of some kind of altruistic behavior? Does it show an enduring commitment of the individuals to each other?

There are certainly occasions when a human being reassures a friend with an encouraging pat on the back because the close proximity of a person in distress is disturbing. His unhappiness intrudes on his companion's sense of well-being and makes him uncomfortable. Thus the comfort given, while it results in calming his friend, may be made at least partially to relieve his own discomfort. It is equally possible that, for a chimpanzee, the sight and sound of a crouching, whimpering, or screaming subordinate may make him feel uneasy. He may have learned that he can calm the other with a touch. We have already mentioned that an agitated chimpanzee may seek reassurance by reaching out to touch a companion—such an action on the part of the uneasy superior would serve the double purpose of calming both.

It is also possible that both the submissive posture of the subordinate and the reassuring touch of the dominant may have originated from social grooming. This is an activity which provides chimpanzees with long periods of relaxed physical contact and, as we shall indicate in a later section, grooming appears to calm apprehensive individuals. Thus, it is possible that the submission-reassurance sequence may be derived at least partially from the social grooming pattern. The crouching might be a ritualized invitation to groom; the touch of the superior a ritualized grooming response. There are, in fact, occasions when a few brief grooming movements do occur in response to submissive crouching.

When two chimpanzees meet after a separation, they may engage in gestures and postures that strikingly resemble forms of human greeting. Chimpanzees may bow, kiss, touch or pat one another, hold hands or embrace. A male may chuck a female or an infant under the chin. In chimpanzee society, reunion after separation often involves behaviors that serve to reestablish the relative social status of the individuals concerned. Originally greeting behavior in man probably served a similar function—and still does on some formal occasions. In general, however, greeting in man has become ritualized in a variety of cultures.

There are similarities, too, in some chimpanzee and human aggressive behaviors. A quick upward jerk of the arm serves as a threat in a chimpanzee,

as does a level stare directed unwaveringly at a subordinate. A chimpanzee may adopt an upright posture when he is threatening and wave his arms above his head, and he may throw objects, overarm and underhand, toward whomever or whatever he is threatening. He may brandish a stick or make a downward clubbing movement. Attacking chimpanzees may bite, hit, and kick. Female chimpanzees sometimes scratch and pull out a handful of hair from their victim's head.

At this point, it should be noted that chimpanzees are not, on the whole, highly aggressive primates in the natural state as compared, for example, with baboons and macaques. Most aggressive incidents occur during status conflicts between males and these rather than taking the form of physical attack usually involve bluff—-vigorous charging displays, often performed bipedally and with hair erect so that the actor looks as large as he can, waving sticks and branches, hurling objects. Two males competing with each other for status may "display" toward and around one another for up to thirty minutes, after which one of them either retreats or approaches and shows submission. Occasionally, such an episode terminates in a serious fight with grossly visible injury. Female fights occur also. Often they begin when squabbles occur during the play sessions of their offspring.

When the chimpanzees at Gombe were fed bananas on a regular basis, this resulted in the crowding together of relative strangers—individuals who

would not ordinarily have met. These chimpanzees were competing for a favored food that was in relatively short supply. During these three years, aggressive incidents rose dramatically both in frequency and in intensity. When regular banana feeding was stopped, the chimpanzees, no longer crowded together in unusually large groups, quickly resumed their less violent way of life. Lee has reported that Kalahari Bushmen who are usually nonaggressive become aggressive when several bands congregate around a water hole in time of drought.

There are some similarities in the play patterns of humans and chimpanzees. Chimpanzees use their fingers in the same way as humans when tickling a playmate, and they respond to intense tickling with sounds not unlike those made by laughing children in a similar context. Chimpanzees turn somersaults and pirouette, and one youngster spent minutes at a time trying to stand on his head. Sometimes he succeeded if there were a nearby tree against which he could balance his feet.

Finally, what of the emotions? Most people who have become well acquainted with chimpanzees agree that these apes almost certainly have "moods" that are similar to those states which, in man, we call sadness, happiness, rage, grief, and jealousy. So far no one has tackled a scientific investigation of these states in the chimpanzee; it will be an extremely difficult though very rewarding area of research.

Some Major Differences in Chimpanzee and Human Behavior; and Possible Selection Pressures Leading in the Human Direction

In this section, we shall discuss several of the more obvious differences between man and chimpanzee that are highlighted by our understanding of chimpanzee behavior: (a) in man hunting became a way of life rather than an occasional luxury; (b) man developed a characteristic bipedal gait; (c) the human female became constantly sexually receptive; (d) humans began to show some forms of contact behavior that differed in some ways from those shown by the chimpanzee; (e) man developed a language in which he could communicate about events past and future and about abstract concepts and theories. In addition, man, at some point in his evolution, lost most of his hair, an occurrence that might have influenced a number of the changes listed above.

Do we find traits in the chimpanzee today that could be precursors of these uniquely human characteristics? In some cases we do and, with our understanding of chimpanzee behavior in the natural habitat together with information derived from the fossil record, we are in a position to postulate some environmental and social pressures that might have shaped such traits in the direction of their present human form, i.e., conditions under which natural selection might have favored evolution from chimpanzee-like behavior in an ancestral stock to humanlike behavior in a later era.

During this discussion we shall refer, from time to time, to a hypothetical group of chimpanzees, or chimpanzee-like creatures, living in an area where gallery forests penetrate bush or savanna country that is fairly rich in prey animals. This will give a picture of a group of beings that are undoubtedly similar in many ways to our own ancestors, living in an environment similar to that which is commonly supposed to have nurtured early man. We must remember that the patterns to be discussed undoubtedly evolved at different times, different rates, and over many thousands of years. In each case, therefore, we are considering an unknown span of time when crucial changes were taking place. We are trying to tease out factors that might have been responsible for changing a quadrupedal, tree-living, mainly vegetarian ape into an upright, savanna-living hunter with a large repertoire of tools and weapons, a more advanced culture, and a language. Whether our hypothetical group of apelike creatures are ancestral to the first true men or early examples of *Homo* himself will probably vary with the aspect of behavior under discussion. Some features considered uniquely human today were probably not yet apparent in the creatures that paleontologists would classify as *Homo,* while other characteristics of man are, as we have seen, present also in the chimpanzee and therefore were undoubtedly present in the common ancestor.

Hunting as a Way of Life

We have already described some of the main hunting, cooperative and food-sharing patterns occurring in the chimpanzee today. Now we are concerned with the possible reasons underlying the change from a mainly vegetarian to a mainly carnivorous diet in early man. This change, if it forced our ancestors to spend more and more time on the savanna away from the comparative safety of the forest, undoubtedly played a crucial role in shaping human evolution. Behaviors most likely to have been influenced directly were the development of killing and cutting tools, cooperation, food sharing, division of labor and bipedal locomotion. In addition, a new environment with its new challenges and dangers undoubtedly placed a high premium on intelligence; individuals who were the most quick-witted in times of sudden danger and who were adept at problem solving were more likely to survive.

Any clues we may derive from an understanding of the carnivorous behavior of the chimpanzee today that might help us toward understanding how and why early man or his ancestors adapted to a hunting way of life will be worthwhile. Firstly, then, we should ask what pressures operating on chimpanzees today might be expected to bring about an increase in hunting behavior. It is important to remember that chimpanzees appear to be extremely partial to meat. This is suggested by the intense excitement that always attends a successful hunt, the persistence of many individuals in trying to obtain a share of the kill, and the eagerness with which almost every scrap of carcass is consumed. Wild baboons also hunt and eat small mammals

and birds with apparent satisfaction; gibbons, gorillas, and orangutans, although so far they have not been observed eating flesh in nature, will readily accept it in captivity. We may, therefore, postulate an inherent tendency among higher primates to accept meat as food.

We should also consider the role of the individual in initiating any new tradition. Some chimpanzees like meat more than others or, at least, they seem to eat it more often. At Gombe, there was one old female who nearly always managed to be at the scene of a kill. She begged persistently and fearlessly from the adult males and nearly always managed to acquire quite large amounts of meat. In this case, at any rate, it seems that her offspring, probably as a result of early and repeated exposure to meat as food, have acquired her extreme interest in it. All of them, ranging from eight to over twenty years, also beg persistently at kills. Moreover, the two adult sons have both been actively involved in many hunts and have both made kills themselves, one of them even while he was still an adolescent and the other even after losing the use of one arm when he contracted poliomyelitis. Other individuals of the same age and sex as these four participate in meat eating and hunting less frequently.

These facts alone mean that it is not inconceivable that a trend toward increased hunting and meat eating might develop quite spontaneously in an area that was slightly richer in easily available prey animals than is Gombe. If,

for instance, just a few individuals of our hypothetical group began to make frequent sorties into the neighboring savanna in search of young gazelle, the habit might, in time, spread through the community. If there was a particularly bad fruit crop one year, this might intensify such a hunting tradition.

There is another factor that might force chimpanzees to hunt more frequently. In the Kasakati Basin area, to the south of Gombe National Park, there is an annual migration of the group being studied. This apparently occurs as a result of the movements of a much larger group. The smaller group moves some twenty miles from the range it inhabits for about three quarters of each year, apparently to avoid the larger and more dominant group as it moves in. In this particular area, the subordinate group simply moves on into another part of its range, which is ecologically very similar to the one it has been forced out of. But it is not difficult to imagine a situation in which such a group might be driven into an area that was ecologically different from its normal range—onto the fringes of the savanna where its very survival might depend on an increase in carnivorous behavior. The competing group might be a larger number of the same species, as is the case in the Kasakati Basin, or it might be of different species with larger or more aggressive individuals.

It is widely accepted today that the earliest men were already hunters. A

great many bones and fragments of bones of animals presumed to have been the prey of *Homo habilis,* together with associated "pebble tools," have been found at living sites at Olduvai by Dr. L.S.B. Leakey and his colleagues. There is evidence suggesting that even the more primitive australopithecines were already hunters. There is, however, some controversy as to whether our ancestors became true hunters only after acquiring a taste for meat by scavenging or whether they were bona-fide hunters from the start. We firmly support the second hypothesis.

Although there is some evidence at Gombe that chimpanzees may seize a freshly killed victim from hunting baboons within a few moments of its capture, the apes normally catch their own prey. When we set out the body of a freshly killed bush pig, the chimpanzees appeared frightened and did not attempt to feed on it. At a time when the chimpanzees were in the habit of snatching domestic chicks for food, a juvenile female, after killing one, left it almost untouched. None of the other individuals who later passed the body touched it. The remains of a young bushbuck, probably caught earlier by baboons, was also ignored by the chimpanzees. Thus it seems that the prerequisites for chimpanzees feeding on flesh may be (a) the excitement attendant upon a kill (whether it be a chimpanzee or a baboon kill) or (b) the sight of another chimpanzee feeding on flesh.

It should be mentioned also that whereas baboons have been observed

in many areas hunting and eating small mammals and birds, as mentioned above, we can find no reference of their scavenging from the carcasses of dead animals. Baboon troops have frequently been observed near the remains of kills on the Serengeti, but they were never seen to form a part of the attendant scavenger group, and in Nairobi Park fresh carrion was ignored.

Let us for a moment consider our hypothetical apes who are beginning to change to a more carnivorous diet, and imagine how they would fare as scavengers. Studies on the Serengeti Plains in Africa vividly reveal some of the problems and dangers attendant on a scavenging way of life. Any appreciable amount of food available for scavenging consists of carcasses of animals that have died a natural death or the remains of the prey of other carnivores. One problem is to find such food. This may be done by sight, hearing, or smell. If the real killer is still finishing his meal, how can one get a share without being hurt? How can one get there before too many other competitors have arrived at the scene? It is not only vultures, jackals, and hyenas who feed on dead flesh—lions and leopards will do so readily.

In many ways the hyena is well adapted for a scavenging role. He has enormously strong teeth and jaws. Thus, he is able to chew extremely large bones and tough hide that he is subsequently able to utilize, thanks to a remarkable digestive system. He has acutely sensitive ears so that he can accurately locate far-off sounds made by other carnivores at a kill. He can run

quite fast and he has great stamina. Yet even he does most of his own hunting. The jackal, too, though he is often successful in obtaining scraps from a kill even under the noses of larger carnivores, thanks to his lightning speed, nevertheless hunts insects and birds most of the time. In fact, the only creatures that are really successful at scavenging are the vultures and other winged carrion eaters. They can maintain vantage points high in the sky and keep watch over large areas of the country. When they see potential food with their exceptionally keen eyes, they can reach it much faster than a creature that must run on the ground. Indeed, it is by closely watching the movement of vultures in the sky that many earthbound predators are directed to available food sources.

Our hypothetical ape, in the process of moving onto the savanna and taking up a more carnivorous diet, might have been a reasonably fast runner, and he might have had great powers of endurance. But even though his hearing was probably keener than that of modern man, it is unlikely that his auditory capabilities could match hyenas or jackals. Nor would his sense of smell have been as acute as theirs. He would have been able to watch the sky for telltale movements of vultures and run to the scene of a kill along with other scavengers. If, on arrival, he had found only vultures there, or perhaps a couple of hyenas and jackals—or even a single lion—he might, if he was with a group of his kind, be able to drive them from their meal and appropriate it for his group. But in those early days when man (or his forebears) was just

starting his hunting life, his weapons were probably nothing more than rocks and sticks, and it is unlikely that a small group of apelike creatures could have driven a large number of hyenas or a pride of lions from their kill. In those early days, there would have been little if any fear of man (found in most wild creatures today) to assist him in driving off competitors. Anyone who has watched the larger carnivores in action—seen a lion killing a hyena at a carcass, watched a group of hyenas chasing a lion from its prey, observed the deadly spring of a leopard—will be only too well aware of the dangers faced by scavengers.

We are not trying to say that, during his development into a hunter, man never scavenged. Man is, and undoubtedly always has been, an opportunist. Our Stone Age ancestors or their predecessors would have scavenged when the reward was worth it and the risks not too great. However, in view of the dangers attendant on scavenging, the difficulties involved, and the total absence of scavenging behavior in living primates today, it seems more reasonable to suppose that most of the meat early man consumed had been killed by his own group. Only when his weapons became more deadly and he had the means of intimidating the larger carnivores, would it have been practical to any great extent for him to try to supplement his meat diet by scavenging from the kills of others.

The environmental conditions favoring greater reliance upon the

savanna need more specific attention. Whatever these may have been, greater reliance upon the savanna would have meant more hunting and this in turn would have placed a premium upon cooperative behavior. As we have seen, cooperation is important in enhancing the effectiveness of chimpanzee hunting, and would probably have been much more important under open country conditions. So, whatever else an increasing reliance upon hunting may have meant for human evolution, we think it gave selective advantage to intelligently cooperative individuals.

Bipedal Locomotion

Man walks and runs in an upright position that is unique among living primates. Many speculations have been put forward as to: (1) the circumstances that might have given rise to the gait, and (2) the various ways it might have affected the subsequent development of man once it had been established.

How frequently does the bipedal stance occur in the chimpanzee today, and in what circumstances is it most likely to occur? For anatomical reasons the chimpanzee is a poor bipedal walker when compared to man: mostly he bends forward at the waist and shows a waddling gait. Usually he only moves for a few yards in this posture after which he resumes his quadrupedal, knuckle-walking gait. There are, however, exceptions to this: there are a few

individuals in our community who walk upright with a posture that is almost that of a man, and one individual shows only the slightest sign of waddling. These chimpanzees tend to move farther in an upright posture than their companions. This suggests that there is ample biological variation in the locomotor system upon which natural selection could operate in a direction toward bi-pedalism, if environmental conditions favored such behavior.

Chimpanzees most often move bipedally when they are carrying food, performing aggressive displays, looking for a companion or some other object in long grass, or traveling over very wet ground. Two chimpanzees learned to travel almost constantly in an upright posture after each lost the use of one arm as a result of contracting a paralytic disease, probably poliomyelitis. One of these chimpanzees, in particular, has adapted to bipedal walking in a very dramatic manner. His posture is very upright, his strides are even, and he can travel in this way for many minutes. After he has taken a couple of tripedal steps using his one sound arm, he resumes the upright posture. In this way he can keep up with other chimpanzees even when they are traveling quite fast.

If our hypothetical group of chimpanzees living at the edge of the savanna only penetrated the grassland for very short distances, very infrequently, it is difficult to imagine that there would be any factors that would strongly select for more frequent adoption of an upright gait. If, however, their excursions from the forest became longer and more frequent,

there would be much advantage for these individuals who were able to walk upright easily. (1) For one thing, they would be able to see over the grass and notice (a) the presence of dangerous carnivores, (b) the whereabouts of potential prey, and (c) the whereabouts of their companions, which would be especially important during cooperative hunting. Such behavior is striking among savanna baboons when they are in tall grass far from trees. (2) If these hypothetical chimpanzees made a kill, they would very likely want to carry the prey back to the forest. Chimpanzees are not equipped for eating meat quickly; moreover, they invariably eat quantities of leaves with flesh. They could carry the prey in a tripedal position, dragging it along the ground or slinging it over the neck or shoulder. But if they could not see over the grass, there would be the danger that some scavenger, such as a hyena, might sneak up and make off with their meat. (3) It is also possible that if the chimpanzees were not hunting but foraging the savanna for roots, berries, or even insects, they might still, particularly if they were close to the forest, return to feed in the safety and shade of the trees. A return journey of this sort would only be worthwhile if they could carry a large amount —that is, in both hands, and thus with a bipedal gait. At Gombe we have seen chimpanzees collecting handfuls of fallen fruit and then moving bipedally to sit and eat the meal in the shade of a tree. (4) Aggressive encounters with potential scavengers when the chimpanzees were still in the grassland would almost certainly result in aggressive bipedal displays. At Gombe encounters with baboons during

competition for bananas at the open, artificial feeding area resulted in some of the most spectacular displays of this sort, when chimpanzees leapt upright in the air, waving their arms and hurling rocks or brandishing sticks. Baboons also eat meat, and we have seen a male baboon at Gombe try to take meat from a chimpanzee.

Thus, encounters with scavengers including baboons would have selected for increasingly vivid bipedal displays, since this form of bluff makes the chimpanzee appear bigger and more dangerous than he really is. Also, the upright posture is by far the best position for efficient throwing and stick wielding. If we envisage a situation in which the chimpanzee was confronted by another species of *ape,* a species that also specialized in bipedal bluff and throwing, then there would be a very powerful selective pressure for increasingly efficient bipedal display and weapon use. It is highly plausible that one of the main threats to early humans arose from other groups of early humans.

In the chimpanzee still another factor would exert a strong selective pressure for the development of bipedal walking—namely, if infants were unable to cling to their mothers. Two factors that might have influenced this in human evolution are: (1) the loss of hair on the mother so that there was nothing for the infant to cling to, and (2) increased brain size necessitating earlier birth since the human pelvis will not permit the birth of a larger head.

Thus, as human evolution progressed, infants were born in an increasingly immature condition, hence less able to cling effectively.

The development of some bipedalism might have been necessary to free the mother's hands sufficiently to hold the baby whose nervous system was too immature for firm clinging. Historically, there must have been a feedback relation among the major components of human evolution. The need to hold the immature, large-brained baby could have been a powerful stimulus to further improvement of bipedalism. We have evidence at Gombe that it is possible for a chimpanzee to adapt remarkably to an upright posture even during the life span of the individual. (We refer here to the two males who began to walk upright after each lost the use of one ann.) We suggest that it could also be possible for females to adapt in this way in order to carry their infants, particularly as this adaptation would take place slowly, over countless years with natural selection favoring those mothers who were effective in holding the infant.

It is frequently suggested that the development of tool use was one of the main factors that gave selective advantage to bipedalism. While we see the logic of this reasoning, we are inclined to think the point has been overemphasized in relation to the early phases of human evolution. As Tobias has pointed out, the ability to sit in an upright position is all that is needed for the hands to be freed for tool use. The chimpanzees at Gombe do indeed carry

out most of their tool-using performances in a sitting posture. Only when the tool-making cultures of early man were sufficiently advanced as to necessitate the carrying of premade tools from one place to another would bipedal locomotion become necessary for tool-using; and, as Leakey has pointed out, early stone tools were usually made on the spot rather than carried from place to place. However, as we have seen, more frequent use of weapons and the development of more sophisticated weapons would certainly give added selective advantage to upright locomotion.

Constant Sexual Receptivity in the Human Female

Another feature that is unique to the human primate is the constant state of sexual receptivity of the female. Other primates in natural habitats mate only during those periods when the female is in estrus or at least close to estrus. The human female is attractive and receptive to males throughout her reproductive life and beyond into the menopausal era. It is very difficult today to imagine a human society in which women were only sexually accessible once a month; and there has been a great deal of speculation as to the circumstances in which this unique development took place.

The most widely accepted suggestion is that a strong sexual bond was *necessary* to ensure that the male would return from his hunting sorties to share meat with waiting women and children and, in return, get his share of

the berries and roots they had gathered during his absence. Once the sexual pattern of constant receptivity had been established, it enabled the formation of the typically human family structure.

It may be meaningful to review briefly the kinds of heterosexual relationships occurring in contemporary nonhuman higher primates, particularly in chimpanzees. The most usual monkey pattern is that in which each female in a troop is mated by a variety of males during at least part of her period of receptivity. In some species a high-ranking male is likely to monopolize her sexually during the peak of estrus—in other words, when she is most likely to conceive. In the hamadryas baboon, the local population is comprised of a number of "one-male groups". In this species, each male acts as "overlord" to a number of females whom he zealously protects from sexual contact with other males of the troop. Nor does he seek sexual satisfaction other than with his own females. This system resembles the harem family group of many human cultures. There is only one example among nonhuman higher primates of a male and female forming a monogamous pair (which may be for life) and that is the gibbon, a small, tree-living Asiatic ape.

In chimpanzee society a variety of sexual behaviors are possible. Sometimes a female may be mated by all the males available throughout her period of genital swelling. Sometimes she may go off with one male during the peak of estrus—the male may vary from one estrus period to the next. And

sometimes a relationship develops in which a female will go off with the same male during successive periods of estrus. This is not to imply that the female will refuse the advances of other males nor that the male will not mate with any other females available to him. It does, however, suggest that there is some incipient tendency toward the formation of stable pair bonds in the species.

However, as female chimpanzees get older their periods of sexual activity become very widely separated. A young female is likely to show periodic swellings, when she is receptive to males, during most of her pregnancy; and she will resume sexual swellings again about two years after the birth of her infant, even though conception has not been known to occur until the previous infant was at least three and a half years old. But older females do not usually become sexually receptive either during pregnancy or until the infant is about four and a half years of age. These older females very frequently move about on their own, with only their dependent young, whereas younger females are much more often with groups of chimpanzees.

While it is not easy to see any particular advantage for the chimpanzees at Gombe in the development of more stable associations between the sexes, this acquires a different significance for our hypothetical chimpanzee group that is moving frequently into the savanna from the forest. In this situation two factors that might select for longer and more frequent periods of sexual

receptivity in the female suggest themselves. In the face of a potentially dangerous object or predator, it is the males who become especially aggressive, leaping about, calling, swaying branches, hurling rocks, brandishing sticks. For a society of chimpanzees cooperative protective bluff —and occasional serious fighting—would, presumably, become increasingly important to survival in the new and more dangerous environment of the grassland, where there are fewer trees and more carnivores. Females and youngsters wandering about far from the protection of adult males would be endangered; those with longer and more frequent periods of receptivity would travel more frequently with adult males and have a greater chance of survival.

We have already mentioned that a receptive female is very likely to obtain a share of meat when she begs from a male in possession of the carcass. If meat became a much more important item of chimpanzee diet—particularly in the face of any shortage of vegetable foods—it would become increasingly necessary for females to obtain adequate shares of each kill.

Previous discussions on the evolution of the unique human female sexual pattern have usually centered around that time in evolution when there already was a clear division of labor: when the men went out hunting and the women stayed behind gathering roots and berries. But there is some overlap in the division of labor—e.g., in some hunting-and-gathering

societies, women take part in the dismembering of the kill, especially if it is a large carcass such as that of an elephant.

If man's early ancestors showed incipient tendencies similar to those shown by the chimpanzees today toward stable pair-bonding, the further strengthening of those bonds between a man and woman would have been complicated by a change in life style from a mainly vegetarian to an increasingly carnivorous diet, from existence in the forest to existence on the grassland. When a male chimpanzee goes off with a female in estrus, they often stay away from all other chimpanzees for seven to ten days. But it might have been unsafe for an early human couple to go hunting alone in the savanna. Also, if meat was really important in the diet of these early ancestors, the pair could ill afford to remain away from the group for over a week each month since, on their own, they might achieve but little success in hunting. Life was difficult, there was probably a greater ratio of females to males as is common in most primate species, and in order to survive, early man could not afford to waste chances of reproduction by mating with one female only. It would have been important that all available females should be fertilized during the early struggle to survive in a new habitat. Thus, the effect of this great evolutionary transition on male-female attachments must have been complex. Our estimate is that it tended to strengthen them, but probably not to create a strictly monogamous society.

One other comment may be made in connection with the evolution of constant receptivity in the human female. There is evidence that social pressures can influence receptivity in some primates. Thus, in a hamadryas baboon society, where the female is forced to leave her mother and join a one-male group when she is only one year old, she develops a sexual swelling and becomes receptive to the advances of her male a whole year earlier than the females of other baboon species.

In the chimpanzee, there are numerous instances in which physiological and psychological stress can inhibit sexual swelling; and there is one case where psychological factors may have led to the development of a swelling. This occurred when an old female in our community was socially grooming with several adult males; suddenly a young female with a sexual swelling arrived. The males at once left the old female and hurried to groom the newcomer. For a few moments the old female simply stared at the young female, all her hair on end (a sign of aggression). Finally, she slowly approached the group and intently inspected the swelling of the other female. The following day, this old female had developed a small swelling, her first in a long time. The swelling was not large enough for any male to mate her, but several males were very interested, hurried up, inspected the swelling and groomed her vigorously as they had groomed the young female the previous day.

This incident is described here because any factors relating to the prolongation of receptivity in our closest relations may be significant to an understanding of the unusual constant receptivity of the human female. It is also worth emphasizing that the chimpanzee has probably progressed further than most other nonhuman primates in increasing the time when a *young* female is sexually receptive. She shows regular recurrent swellings for two to three years before she has her first infant; she continues to show cyclic swellings during six to seven months of her eight month pregnancy; and she may swell again when her infant is only fourteen months old, despite the fact that she will not conceive for another two and a half to three and a half years. It has been suggested that periods of estrus in baboons would be incompatible with caring for an infant owing to the complete disruption of other social patterns during that time. Among the chimpanzees, a mother continues to care adequately for her infant during repeated periods of sexual receptivity.

In captivity, when a chimpanzee male and female are housed together in a small cage with nothing to do, the male may copulate even when the female is anestrus and her sex skin is flat. In similar laboratory conditions, rhesus monkeys also show an extension of the period in which copulations occur. Thus, it is possible that the evolution of a stronger bond between couples, with its enhancement of proximity, may in itself have provided conditions favoring extended receptivity in the women of early human societies.

Social Grooming

Social grooming, in which one individual looks through the hair of a companion and extracts, with lips or fingers, small flakes of dry skin, parasites, and so on, plays a very important role in the social life of most of the higher nonhuman primates. Chimpanzees may spend up to two hours in sessions of social grooming; these tend to be longest and most frequent between close associates such as adult males who travel around together, mothers and their older offspring, and some couples. Social grooming thus provides long sessions of relaxed, physical contact between friendly chimpanzees. Grooming also occurs in other contexts: it may serve to calm an excited or frightened chimpanzee and it is frequently seen during a greeting between two individuals or in response to a submissive present.

If our earliest human ancestors still had a fairly abundant supply of hair, it is almost certain that they, along with the other higher primates, would have groomed one another. But what would have happened when they gradually—or suddenly—lost their hair? For a while social grooming would undoubtedly have continued, first because of the important role it had played for so long, and second because there still are several hairy places left to groom on the unclothed body. Most of man's hairy patches, however, are not those parts of the body which are most frequently groomed by chimpanzees. Moreover, during a long grooming session between two chimpanzees each

individual often searches through his companion's hair quite systematically, covering most of the body. With grooming restricted to the few parts of the human body that are fairly luxuriant in hair growth, a session could not be protracted except by covering the same areas time and again.

Perhaps for a while early man continued to make grooming movements on those places where it most pleased his companions to be groomed, even if they were areas such as the back, shoulders, and thighs, where there might have been very little hair. In time, however, such behavior might have become simply stroking movements. In place of the lips picking out small flakes of skin from the hair, kissing might have become more frequent. Individuals bored by stroking their hairless companions, might have merely laid their hands on the back or shoulders of their partners, and sat together in companionable, close physical contact. They might have held hands.

Social grooming, as such, has not disappeared entirely from the human repertoire. Waika Indians show intense mouthing of each other's skin during greetings, particularly of the face, and this behavior may well have derived from grooming with the lips. Combing, brushing, or arranging a partner's hair, or searching for lice, may occupy some portion of each day in some cultures. There are many other examples of grooming activities, particularly between mothers and their young children and between young couples.

All these activities, however, play a relatively minor role in the social life of our own species. Yet in man, as in the chimpanzee, there is a need for friendly physical contact between closely associated individuals. What forms of contact behavior have we developed in place of social grooming?

In many cultures friends or close companions will hold hands, put their arms around each other's shoulders, or link arms. In many human societies such behavior is quite common between males despite the fact that, in Western culture, it is likely to be frowned upon. In heterosexual love relationships, touch, in the form of caressing, holding, and kissing, plays a very important role. Often, indeed, this kind of behavior may be as important to the feeling of well-being as sexual intercourse. And these are all forms of contact behavior which are almost entirely lacking in chimpanzees, though occasionally a mother may lay her hand on her child's back, or hold his hand for a while, and he may do the same. For the most part, in chimpanzee society, friendly contact is expressed in social grooming.

Human Language

Language, above all else, stands out as a unique evolutionary achievement of our own species, for it is chiefly through language that so many other human characteristics have been developed and refined—characteristics such as love, religion, self-respect as well as the most complex

intellectual activities. While one may find simple precursors of such characteristics in the chimpanzee, without language it is impossible to conceive of their appearance in human form.

The chimpanzee has a large vocabulary of calls, each of which serves to convey specific information as to the context in which the call is given and the identity of the chimpanzee making the sound. Loud grunts are given when a chimpanzee finds a succulent food source; other chimpanzees can correctly interpret the calls, hurry along, and join in feeding. A youngster is attacked and screams; his mother hurries to the scene and defends him or provides support; but she will ignore the screams of another youngster of the same age and sex as her own offspring.

Recent research into the brain circuitry relating to speech suggests that the calls of the chimpanzee are not the direct precursors of human spoken language. The neurobiology of speech is undergoing major clarification. In considering the evolution of language, this is not the place to discuss the existing "vocabulary" of the chimpanzee. Instead we should look for circumstances that might have placed a very high premium on the need for a more precise exchange of information.

Until recently it was believed that chimpanzees were unable to learn to talk partly because of deficiencies in the vocal apparatus but mainly because

of their inability to conceptualize and think in abstractions. Current experimentation on teaching chimpanzees language by means of signaling or the use of plastic symbols indicates that the chimpanzee's capacity for concept formation has been underestimated. The young chimpanzee Washoe, trained in sign language by the Gardners, was able to recognize and identify her reflection in a mirror, thus indicating that the chimpanzee has at least a crude realization of "self." Another chimpanzee, Sarah, trained in the use of plastic word symbols, showed that she could grasp the meaning of an abstraction. She was taught that blue was a color and that red was a color. She was then able to work out for herself that green was also a color. Other research of this kind is steadily increasing our appreciation of the intellectual ability of the chimpanzee.

The development of hunting behavior in early man might have placed a high premium on the use of sounds that could be used to identify specific places and things. They suggested that the first word may have been the name of a place where the group, having split into hunting parties, would meet in the evening. In addition to this possibility, other factors are worth considering. If man had evolved to the point where he could plan ahead to a meeting in the evening, he would probably have begun to use at least temporary shelters and would be likely to return there habitually. Washburn and Lancaster have also suggested that as hunting increased it would have provided further selective advantage for the evolution of language. For it

would have become more and more useful to communicate subtleties of the hunt for maximum cooperation. This could well be true, but many nonhuman animals have reached high levels of cooperation in hunting without the use of a spoken language. Moreover, while hunting, the Australian aborigines and the Kalahari Bushmen communicate by an elaborate series of signs—the kind of "language" that, as the experiments with Washoe suggest, might have evolved in the chimpanzee more readily than spoken language.

Bigelow makes a similar point in relation to competition between early human groups. The need to defend themselves against enemies in order to survive must have put a premium on cooperation, and the efficacy of sustained cooperation might well have been enhanced by the advent of language. Here as elsewhere, multiple environmental pressures may coincide in a way that strengthens the selective advantage of a particular capacity. In the case of a truly remarkable capacity such as language, it seems likely that several advantages may well have coincided in a way that fostered its evolution. Therefore, we wish to suggest an additional set of circumstances that might have placed a high premium on the development of language.

Hayes raised an infant chimpanzee from birth for the specific purpose of trying to teach her to talk. At the end of four years, Vicki's only accomplishments were softly uttered sounds that approximated papa, mama, and cup. The observers noted that it was exceedingly difficult for Vicki to

make a sound—any sound—that was not directly induced by an accompanying emotion. To make a sound when she *saw* a plate of food was automatic; to make a sound when asked if she would like a plate of food was almost impossible for her. Yet the recent work with Sarah and Washoe demonstrates that the chimpanzee is quite capable of asking for things by gesture or of using plastic word symbols.

Let us now ask what circumstances might have arisen in evolution that would put a very high pressure on the uttering of sounds *not* associated with a sudden emotion? The chimpanzee infant, clinging to its mother and in close contact with her, utters very few sounds. But what if the infant were unable to cling to the mother? Unless the mother was already able to transport the baby in some kind of sling, she would have to put it down occasionally while she did other things. Such a situation might have arisen for the first time with the loss of extensive body hair. Or, if bipedal locomotion occurred earlier in evolution than the loss of hair, this would also produce an infant that was unable to cling to its mother, as Washburn has pointed out; for this led to a changed anatomy of the foot that would no longer permit hair gripping.

In a situation of this sort, there would be a very high premium on vocal communication between a mother and her infant. The contemporary chimpanzee mother and very young infant seldom utter sounds when communicating other than the occasional soft call of the baby as it searches

for a nipple or feels its grip slipping—and the occasional distress scream which the infant may utter on falling or being startled. To both of these sounds, the mother may respond with a similar soft call.

If our hypothetical infant were lying on the ground while the mother was busy nearby and it uttered a cry of distress, the mother would very likely rush over to gather it up, probably uttering a sound herself. The sound would be an integral part of her emotion. But if the infant just gave a soft call, indicating that it was a little hungry or uncomfortable, there might well be a new element emerging in the pattern of mother-infant communication. The mother might want to make a reassuring sound even though she was not experiencing distress to indicate that she would come in a moment. As a result of the sound the baby might be quiet. Without that sound, it might call more and more loudly. In coping with the problems of a changing way of life, the mother might urgently need some way of communicating to her child that she was going away briefly but would be coming back soon: perhaps some way of telling him that if he made a noise he would attract prowling hyenas or lions.

Nowhere do we see more subtle, constantly changing and developing communication cues than between a mother and her growing infant; nowhere do we find a stronger affectionate bond. Many, if not all, of the communication signals used by adult chimpanzees are fundamentally learned in this mother-

child relationship, though some are elaborated later in life. Thus, it seems logical to search for the evolutionary origin of language partly in this adaptively crucial relationship. Perhaps “Mummy” or “quiet” or “coming” would be just as likely candidates for the first spoken words of a new language as the naming of a place or a thing.

Concluding Comments

From our knowledge of the chimpanzees today, we cannot reconstruct the kind of society in which early man lived, nor can we determine the exact nature of his family structure. But we can assume that there were enduring affectionate bonds between a mother and her offspring, and between brothers and sisters. We can be confident that early man had a long childhood during which he explored his environment in play and learned the traditional behavior patterns of his group through watching and imitating and practicing the behavior of his elders.

We can be reasonably certain that early man went through a period of biological and social adolescence during which the male increasingly took his place in hunting groups and learned the hunting techniques of the grown males, while the female spent much time in female society, probably with her mother, and helped to look after her own small brothers and sisters and sometimes the infants of other females of her group.

These early ancestors must have used simple tools of grass and stick and leaves before they developed any kind of sophisticated stone-or bone-tool cultures, and they must have been capable of fairly well-organized cooperative behavior when they hunted for small animals.

When they were frightened, they probably held hands and embraced each other. After quarreling or fighting they made up with a reassuring pat or clasp of hands. When they met again after separating, they kissed and embraced and held hands. They probably groomed each other for hours during their leisure time, or, as their hairy covering receded, made grooming-like movements such as stroking each other.

In short, we have indicated a variety of reasons why the behavior of early humans must have resembled that of contemporary chimpanzees in important respects. A chimpanzee-like ancestor, common to *Homo sapiens* and to contemporary chimpanzees, must have had much genetically based behavioral variability in its populations. Some of this variability was inclined toward patterns of behavior characteristic of man—such as bipedalism and constant sexual receptivity. Drastic changes in environmental conditions, acting over long periods of time, must have given selective advantage in survival to some patterns in the "behavior pool" more than to others. We have tried to suggest some ways in which these steps toward man might plausibly have been facilitated—in light of rapidly emerging new facts in research on

human evolution. Despite this recent progress, many serious information gaps remain. We hope this paper will serve as a stimulus to those interested in the quest for man's origins and the fundamental nature of the human species. This is an old quest, perhaps as old as man himself with all his insatiable curiosity. But today the opportunities for understanding are far greater than ever before, and the urgency of the task is greater as well.

Bibliography

Albrecht, H. and S. C. Dunnett. *Chimpanzees in Western Africa*. Munich: R. Piper and Co., 1971.

Bandura, A. Aggression, *A Social Learning Analysis*. Englewood Cliffs, New Jersey: Prentice-Hall, 1973.

Beatty, H. "A Note on the Behavior of the Chimpanzee," *J. Mammal*, 32 (1951), 118.

Bigelow, R. *The Dawn Warriors*. Boston: Atlantic-Little, Brown, 1969.

----. "The Evolution of Cooperation, Aggression and Self-Control," in *Nebraska Symposium on Motivation*, 1972. Lincoln: University of Nebraska Press, 1972.

Birdsell, J. B. *Human Evolution*. Chicago: Rand McNally, 1972.

Boelkins, R. C. and A. P. Wilson. "Intergroup Social Dynamics of the Cayo Santiago Rhesus (Macaca mulatta) with Special Reference to Changes in Group Membership by Males," *Primates*, 13 (1972), 125.

Bowman, R. I. "Morphological Differentiation and Adaptation in the Galapagos Finches," *Univ. Calif. Berkeley, Publ. Zoo*., 58 (1961), 1.

Brewer, S. In preparation.

----. Personal communication.

Campbell, B. G. "Conceptual Progress in Physical Anthropology: Fossil Man," *Annu. Rev. of Anthropol*., 1 (1972), 27-54.

Clark, J. D. *The Prehistory of Africa*. New York: Praeger Publishers, 1970.

Coon, C. S. *The Hunting Peoples*. Boston: Atlantic-Little, Brown, 1971.

Dart, R. A. "Carnivorous Propensity of Baboons," *Symposium Zoological Society London*, 10 (1963), 49-57.

DeVore, I. and K. R. Hall. "Baboon Ecology," in I. DeVore, ed., *Primate Behavior: Field Studies of Monkeys and Apes*. Boston: Holt, Rinehart and Winston. 1965.

DeVore, I. and S. L. Washburn. "Baboon Ecology and Human Evolution," in F. C. Howell and F. Bourliere, eds., *African Ecology and Human Evolution*, Viking Fund Publications in Anthropology, No. 36. New York: Wenner-Gren Foundation, 1963.

Eibl-Eibesfeldt, I. *Ethology: The Biology of Behavior*. New York: Holt, Rinehart and Winston, 1970.

Gardner, B. T. and R. A. Gardner. "Two-Way Communication with an Infant Chimpanzee," in A. Schrier and F. Stollnitz, eds., *Behavior of Non-human Primates*. New York and London: Academic Press, 1971.

Geschwind, N. "The Organization of Language and the Brain," in S. L. Washburn and P. Dolhinow, eds., *Perspectives on Human Evolution 2*. New York: Holt, Rinehart and Winston, Inc., 1972.

Gombe Stream Research Center Records.

Goodall, J. van Lawick. "The Behavior of Free-Living Chimpanzees in the Gombe Stream Area," *Anim. Behav. Monog*. I, 3 (1968), 161-311.

----. "Tool-Using in Primates and Other Vertebrates," in D. S. Lehrman, R. A. Hinde, and E. Shaw, eds., *Advances in the Study of Behavior*, Vol. 3. New York: Academic Press, 1970.

----. *In the Shadow of Man*. Boston: Houghton Mifflin, 1971.

----. "The Behavior of Chimpanzees in Their Natural Habitat," *Am. J. Psychiatry*, 130 (1973), 1-12.

----. "Cultural Elements in a Chimpanzee Colony," in E. W. Menzel, ed., *Precultural Primate Behavior*. New York: Karger, 1974.

Halperin, S. "Aggressive Behavior of Free-Ranging Chimpanzees." St. Louis: Washington University, Ph.D. Thesis. Unpublished.

Harding, R. S. O. "Predation by a Troop of Olive Baboons (*Papio anubis*)." Paper delivered at 4th International Primatological Congress, Portland, August 1972. Published in *Proceedings of the Congress, Am. J. of Phys. Anthropol*., 38 (1973). 587-592.

Hayes, C. *The Ape in Our House*. New York: Harper and Row, 1951.

Holloway, R. L. and E. Szinyei-Merse, "Human Biology: A Catholic Review," in J. Siegel, ed., *Biennial Review of Anthropology*, 1971. Stanford: Stanford University Press, 1972.

Howell, F. C. "Hominidae," in *McGraw-Hill Yearbook of Science and Technology*. New York: McGraw-Hill, 1971.

----. "Recent Advances in Human Evolutionary Studies," in S. L. Washburn and P. Dolhinow, eds., *Perspectives on Human Evolution 2*. New York: Holt, Rinehart and Winston, 1972.

Imanishi, K. "The Origin of the Human Family: A Primatological Approach," in S. A. Altmann and Yerkes Regional Primate Center, eds., *Japanese Monkeys*. Alberta: University of Alberta Press, 1965.

Izawa, K. and J. Itani. *Chimpanzees in Kasakati Basin, Tanzania*, Kyoto: Kyoto University Press, 1966.

Jones, C. and J. Sabater. "Sticks Used by Chimpanzees in Rio Muni, West Africa," *Nature,* 223 (1969), 100-101.

Kano, T. "Distribution of the Primates on the Eastern Shore of Lake Tanganyika," *Primates*, 12

(1971), 281-304.

Kawabe, M. "One Observed Case of Hunting Behavior Among Wild Chimpanzees Living in the Savanna Woodland of Western Tanzania," *Primates*, 7 (1966), 393-396.

Kawai, M. "Newly Acquired Precultural Behavior of the Natural Troop of Japanese Monkeys on Koshima Islet," *Primates*, 6 (1965), 1-30.

----. "On the System of Social Ranks in a Natural Troop of Japanese Monkeys: Basic Rank and Dependent Rank," in S. A. Altmann and Yerkes Regional Primate Center, eds., *Japanese Monkeys*. Alberta: University of Alberta Press, 1965.

Khroustov, H. F. "Formation and Highest Frontier of the Implemental Activity of Anthropoids," *7th Int. Congr. Anthropol*., Moscow, 1964.

Kohler, W. *The Mentality of Apes*. New York: Harcourt, Brace, 1925.

Kummer, H. *Social Organization of Hamadryas Baboons*. Chicago: University of Chicago Press, 1968.

Lee, R. B. and I. DeVore. *Man the Hunter*. Chicago: Aldine, 1968.

Masland, R. L. "Some Neurological Processes Underlying Language," in S. L. Washburn and P. Dolhinow, eds., *Perspectives in Human Evolution 2*. New York: Holt, Rinehart and Winston, 1972.

McGinnis, P. R. *Patterns of Sexual Behavior in a Community of Free-Living Chimpanzees*. Ph.D. dissertation. University of Cambridge, 1973.

McGrew, W. C. and C. E. G. Tutin. "Chimpanzee Dentistry," *J. Am. Dent. Assoc*., 85 (1972), 1198-1204.

Menzel, E. W. "Spontaneous Invention of Ladders in a Group of Young Chimpanzees," *Folia Primatol*., 17 (1972), 87-106.

Merfield, F. G. and H. Miller. *Gorillas Were My Neighbors*. London: Longmans, 1956-

Napier, J. *The Roots of Mankind*. Washington: Smithsonian Institution Press, 1970.

Nishida, T. "The Social Group of Wild Chimpanzees in the Mahali Mountains," *Primates*, g (1968), 167-224.

Nishida, T. and K. Kawanaka. "Inter-group Relationships Among Wild Chimpanzees of the Mahali Mountains," *Kyoto Univ. Afr. Stud*., 7 (1972), 131-169.

Premack, D. "Language in Chimpanzees?" *Science*, 172 (1971), 808-822.

Pusey, A. Personal communication.

Raleigh, M. J. and S. L. Washburn. "Hu man Behavior and the Origin of Man," *Impact of Science on Society*, 33 (1973), 5-14.

Ransom, T. W. "Ecology and Social Behavior of Baboons in the Gombe National Park." Ph.D. thesis. University of California, Berkeley, 1972. Unpublished.

Robinson, B. W. "Anatomical and Physiological Contrasts Between Human and Other Primate Vocalizations," in S. L. Washburn and P. Dolhinow, eds., *Perspectives in Human Evolution 2*. New York: Holt, Rinehart and Winston, 1972.

Sade, D. S. "Inhibition of Son-Mother Mating Among Free-Ranging Rhesus Monkeys," *Science Psychoanalysis*, 7 (1968), 18-38.

----. "A Longitudinal Study of Social Behavior of Rhesus Monkeys," in R. Tuttle, ed., *The Functional and Evolutionary Biology of Primates*. Chicago: Aldine, Atherton, 1972.

----. "Some Aspects of Parent-Offspring and Sibling Relations in a Group of Rhesus Monkeys, With a Discussion of Grooming," *Am. J. Phys. Anthropol*., 23 (1965), 1-18.

Savage, T. S. and J. Wyman. *Boston J. Nat. Hist*., 4 (1843-44), 383.

Schaller, G. *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press, 1963.

Schultz, A. "Some Factors Influencing the Social Life of Primates in General and Early Man in Particular," in S. L. Washburn, ed., *Social Life of Early Man*. Chicago: Aldine, 1963.

Sperry, R. W. "Mental Unity Following Surgical Disconnections of the Cerebral Hemisphere," in S. L. Washburn and P. Dolhinow, eds., *Perspectives in Human Evolution 2*. New York: Holt, Rinehart and Winston, 1972.

Sugiyama, Y. "Social Behavior of Chimpanzees in the Budongo Forest, Uganda," *Primates*, 10 (1969), 197-225.

Suzuki, A. "Carnivority and Cannibalism Observed Among Forest-Living Chimpanzees," *J. Anthropol. Soc. Nippon*., 79 (1971), 30-48.

----. "On the Insect-Eating Habits Among Wild Chimpanzees Living in the Savanna Forest of Western Tanzania," *Primates*, 7 (1966), 481-487.

Teleki, G. "The Omnivorous Chimpanzee," *Sci. Am*., 228 (1973), 1.

Tobias, P. V. "Australopithecus, Homo habilis, Tool-Using and Tool-Making," *S. Afr. Archaeol. Bull*., 20 (80), IV (1965), 167-192.

van Lawick-Goodall, J. see Goodall, J. van Lawick.

van Lawick, H. and van Lawick-Goodall, J. *Innocent Killers*. Boston: Houghton Mifflin, 1970.

Washburn, S. L. "Human Evolution," in T. Dobzhansky, M. K. Hecht, and W. C. Steere, eds., *Evolutionary Biology*, vol. 6. New York: Appleton-Century-Crofts, 1972.

Washburn, S. L. and I. DeVore. "Social Behavior of Baboons and Early Man," in S. L. Washburn, ed., *Social Life of Early Man*. Chicago: Aldine. 1963.

Washburn, S. L. and R. S. O. Harding. "Evolution and Human Nature," in D. A. Hamburg and H. K. H. Brodie, eds., *American Handbook of Psychiatry*, Vol. 6, 2nd ed., New York: Basic Books, 1975.

Washburn, S. L. and C. S. Lancaster. "The Evolution of Hunting," in S. L. Washburn, and P. C. Jay,

eds., *Perspectives on Human Evolution 1*. New York: Holt, Rinehart and Winston, 1968.

Washburn, S. L. and E. R. McCown. "Evolution of Human Behavior," *Social Biology*, 19 (1972), 163-170.

Washburn. S. L. and S. C. Strum. "Concluding Comments," in S. L. Washburn and P. Dolhinow, eds., *Perspectives in Human Evolution 2*. New York: Holt, Rinehart and Winston, 1972.

Weiner, J. S. *The Natural History of Man*. New York: Universe Books, 1971.

Wrangham, R. In preparation.

----. In press.

----. Personal communication.

Wright, R. V. "Imitative Learning of a Flaked Stone Tendency—The Case of an Orang Utan," *Mankind*, 8 (1972), 296-306.

Yerkes, R. M. *Chimpanzees. A Laboratory Colony*. New Haven: Yale University Press, 1943.

Yerkes, R. M. and J. H. Elder. "Oestrus, Receptivity and Mating in the Chimpanzee," *Comp. Psychol. Monogr.*, 13 (1936), 5-45.

Yerkes, R. M. and A. W. Yerkes. *The Great Apes*. New Haven: Yale University Press, 1929.

Notes

1We are very grateful to the Grant Foundation and the Commonwealth Fund for making this work possible.

2Some individuals regularly raid birds' nests for eggs and fledgling birds, but although small rodents and reptiles may be killed, no chimpanzee has been seen feeding from them.