Recent Evidence on the Evolution of Aggressive Behavior

by David Hamburg

Whatever adaptive functions aggressive behavior may have served in man's past, there is serious question about its utility now.

Why study animals if we wish to understand man? We do this primarily to obtain an evolutionary perspective in which we hope to perceive how man came to be the way he is, and to search for subtle legacies of his ancient past that may be carried with him through both biological and social transmission. We deal mainly with broad trends in evolution—asking whether certain characteristics of vertebrate, mammalian, and primate organisms are maintained or may even become more prominent as we come closer to man. If we find certain characteristics that appear to be especially important in the adaptation of man's closest relatives, then we must look in man to see whether these characteristics are present in him, too, albeit in some complex and obscure way. Such a search also tends to highlight man's distinctive and even unique features, such as language.

Animal behavior may be investigated not only in the laboratory, but also in artificial colonies or in natural habitats. The kinds of information gleaned from each setting are complementary, and all are necessary if the complex roots of behavior are ever to be understood.

Despite recent interest in the subject, very few field studies of primate behavior have focused primarily on aggressiveness. For this reason Eric Hamburg and I undertook a brief field study of aggressive behavior in chimpanzees and baboons in East Africa. We were very fortunate in getting more than 200 hours of close-range observation. We also had generous access to the files of the unique chimpanzee study in Tanzania conducted by Jane Goodall since 1960. With help from her and from another experienced field worker, Phyllis Jay Dolhinow of Berkeley working in Kenya, we acquired a good deal of data on aggressive behavior in the two species.

By aggressive behavior, in this context, we mean threat and attack patterns. We try to describe such patterns, the conditions under which they are likely to occur, and the circumstances in which they are likely to be diminished or terminated, particularly by means of interanimal communication. We chose chimpanzees because they are man's closest living relatives. Their social behavior is as close to that of man as we can find in nature.

Goodall's study is already a classic. She has described a remarkable repertoire of closely linked, usually sequential classes of behavior—aggression, submission, reassurance —with a rich variety of patterns within each class. The similarity of many of these patterns to those of humans is more impressive than the similarity of such patterns in any other nonhuman primate species.

What are the conditions under which the threat and attack patterns occur in chimps? From Goodall's observations and our own, I would summarize them briefly this way.

1. Competition over food, especially that which is highly desirable, spatially concentrated, or in short supply.
2. Defense of an infant by its mother.
3. A contest over dominance prerogatives of two individuals of similar social rank.
4. Redirection of aggression—that is, downward in the hierarchy (such as when a low-ranking male, who has been attacked by a high-ranking male, turns to attack an individual in turn subordinate to him).
5. A failure of one animal to comply with a signal given by the aggressor.
6. Strange appearance of another chimp—for example, one whose lower extremities became paralyzed during a poliomyelitis outbreak.
7. Change in dominance status over a period of time, especially among males.
8. The formation of consort pairs at the peak of estrus. In the early part of estrus, when the female first becomes sexually receptive in each cycle, she copulates very freely with many males, including some of the older infants. But as she reaches the peak of estrus, she goes into a consort pair with one of the highly dominant males, and they go off together for some time (a few hours for baboons, about a week for chimps).

Goodall also reported recently on the development of aggressive patterns during the early years of life. For

example, a ten-month-old male infant has been filmed by Hugo van Lavrick showing typical threatening gestures in a context similar to those of an adult threat. These early aggressive patterns are much more characteristic of males than of females—and this is true of a great many primate species. Kinship is also important in the development of such behavior. A juvenile may threaten or attack chimps older than itself provided that its mother is near and that the mother's rank is higher than that of the victim. Adolescent males are often aggressive toward females when no higher ranking males are present, but they apparently restrain such behavior toward females when dominant males are present. As adolescent males mature, they tend to threaten the lowest ranking mature males and so gain admittance to the hierarchy of adult males. In general, adolescence is a turbulent, aggressive period among these chimpanzees.

The chimp community we studied at the Gombe Stream consists of about 50 animals. They live in a forested valley with open woodland high up. Over the ridges on both sides there are other groups of chimps. Very little is known about their contacts with the communities on the other sides, although such information as is available indicates that contact, when it does occur, is pretty tense.

Our chimp community breaks up in subgroups, most commonly three to eight animals, and sometimes even individual animals for short periods. Composition is rather fluid, although there are certain enduring groups such as the unit of a mother and one or more of her offspring.

One of the characteristics of aggressive display by adult male chimps is that their hair stands out, making the animals look bigger and more impressive. As part of the display a male may drag a palm frond, brandish it over his head as he runs, swing it, or even throw it at somebody.

An adult male who has been away from his particular subgroup for a day usually puts on one of these aggressive displays when he returns. It is very interesting that something like a decay of familiarity seems to occur in many primate species; a brief absence elicits patterns that one sees in more full-blown form with total strangers.

We observed and photographed behavior suggesting that "technical ingenuity" in aggressive displays may be a significant part of dominance behavior in chimps. Three years prior to our study, a large can had been left outside by the research workers. One of the males, named Mike, had at that time incorporated it in his display. He ran at it,

An aggressive display by a dominant chimp causes a frightened young male to climb 40 feet up a tree.

An adult male who has been away from his subgroup for a day usually puts on an aggressive display when he returns.

Here an adult male breaks off from a tense situation with another adult and attacks a mother with a ten-month-old infant clinging to her, giving her a severe beating. High-ranking males usually do not fight with each other.

In an effort to get a share of some preferred food, an experienced female approaches with arm extended, palm up, "fear face," and making a very distinctive panting. Her very slow, ambivalent approach may get her a bit of food.

hit it, started it rolling, and chased it. This action had a tremendous effect on the other chimps, and he very rapidly became the most dominant male—with much less fighting than is typically the case in dominance changes of this kind. Evidently there was nothing in chimp evolution to prepare them for the kinds of sights and sounds that he created with such displays. Three years later—with no intervening episode—we put the can back outside. We were curious about whether he would respond, and how long it would take him. It took him less than ten seconds from the time the can was put down on the ground to the time he took off after it and put on a similar display. All eight other animals within observation at the time ran off into the forest or went up trees. One young male climbed 40 feet and remained in the tree for eight minutes.

Bananas are made available from time to time as a very attractive dietary supplement for both chimpanzees and baboons in the area. These are tense occasions when a good deal of threatening goes on between males of similar rank. What happens typically is that one of them will break off prior to fighting (usually high-ranking males do not fight each other) and attack a smaller, weaker, or less mobile animal. We saw one of those adult males attacking a mother with a ten-month-old infant clinging to her, giving her a severe beating, mainly with his fists and forearm. He did this to the same mother-infant pair three times within a week in these situations of redirected aggression. On one occasion he actually knocked them out of a tree from a height of about 30 feet. Thus, the infant, though generally treated with great tolerance, is not always immune in these episodes of redirected aggression.

After a dominant male has established his control of the bananas, other chimps may try to get him to share with them. An experienced female, for example, may back up to him in a lowered posture. This is called presenting, and it is common in a number of primates in agonistic situations. After she gets up to him, he may put his arm around her waist and give her a hug or a pat on the head.

In the same situation a female might approach with arm extended, palm up, "fear-face," and making a very distinctive panting sound. The approach is ambivalent—three steps forward, two back, three forward, two back. It may take several minutes to cover about 30 feet. Again, he may pat her, and sometimes permit her to take a bit of banana.

In the middle of the day, even after a very tense, agonistic morning, a group of animals tends to seek proximity. They have the whole valley to choose from, but they seek out each other's company and move in close to each other for a rest.

The most organized hunting pattern known in any nonhuman primate has been described in the Gombe Stream area. Typically, this occurs when an infant baboon (or colobus monkey) gets isolated up a tree. One adult male chimp goes up after it, and two or three other chimps surround the base of the tree to fight off any adult male baboon who tries to defend that infant. If the chimps catch the infant, the male in the tree and the next one up will tear it apart, and two or three of these high-ranking males will begin to eat it immediately. There is enormous excitement as other chimps arrive and beg in the most extreme way for just a tiny bit. But if the same kind of animal is put out—freshly killed for experimental purposes— there is nothing like the excitement induced when they do their own killing, and they do not eat the carcass.

At the same time as chimp-chimp interactions are occurring, the chimps and baboons are contesting too, as for example when we made bananas available after about a week's absence. The two species clearly know each other well; the chimps are generally dominant over the baboons in this setting. Members of both species were anxious to get the bananas. Two highly dominant chimps, Mike and Goliath, got them most often. It was common to see an adult male baboon giving Mike a strong threat—a display of his canine teeth. Other male baboons join in the fray. The baboon technique is one of harassment, and they may keep up the pressure for a couple of hours. Now and again they get a banana peel, but not much more.

Despite a few baboon threats, Mike appeared to be so relaxed that he stretched out with a pile of bananas right by his belly. The baboons, smaller than the chimps but with enormous canine teeth, kept close by, frequently threatening. As they persisted in this menacing behavior, Mike's relaxation disappeared. He gathered up a bunch of bananas, put them on his lap, and sat on one of the banana boxes. (Often, if a banana is put down momentar-

1. When bananas are made available, chimps and neighboring baboons try to get the fruit. Usually, as here, the highly dominant male chimps get it, but the adult male baboons stay nearby, threatening.

2. Despite the baboon threats, one of the most dominant chimps is so relaxed that he stretches out with a pile of bananas right by his belly.

ily, a baboon will dash in close and grab for it and then dash away again.)

Finally, after about five minutes more, a baboon broke off and attacked an adult female chimp rather than one of the male chimps he had been threatening. She went up the tree, as fast as she could, and he went after her. Once in the tree she started striking down with her fist and hit him on the snout; and he came back down bleeding. No male made any effort to defend her, although in similar situations there is a good chance that a male would come to an infant's defense.

Infants, of course, eventually learn to defend themselves, and we observed one way they learn. We saw an older infant chimp (in the company of another chimp) wielding a ten-foot palm frond like a baseball bat against an adult male baboon that could certainly kill the infant in an isolated situation. He hit the baboon with good accuracy, and chased him off into the forest. What's interesting is that for two years this infant observed two older siblings in exactly this kind of behavior. Both older siblings were quite skillful in using palm fronds as weapons. The infant practiced that behavior initially in the most clumsy way after observing them at length, and he eventually perfected the skill at age 4, which is still a very young chimp. (They do not fully mature until 10 or 12.)

It is often said that the cues in all species but man are so clear and sharp that aggressive interactions can be fine-tuned so that serious injury hardly ever occurs. This is largely correct, but there's a tendency to exaggerate the point. When evidence of serious injury has been looked for systematically in recent primate field studies, it has been found to be rather more common. The cues that limit aggression usually work, but not always.

Grooming—taking the fingers and lips and going down through the hair to the skin in a deliberate, repeated way—is an important behavior pattern in limiting aggression. The high-ranking males get groomed a lot, but they tend to groom others rather less. In any case, grooming seems to have some kind of tension-relieving effect, whatever other hygienic functions it may have. Similarly, an experienced female can sometimes calm an excited, aggressive male by touching his scrotum.

3. *But as the threats of the baboons persist, the chimp, now less relaxed, gathers up his bunch of bananas and sits on one of the banana boxes, holding the fruit in his lap.*

Observational learning in a social context seems to be the principal mode of learning for the nonhuman primates.

Baboons are also present in the forest habitat. We wanted to compare these forest baboons with baboons living in a savanna (plains) habitat.

There are several reasons to study baboons. One is the adaptive process of the closely related baboon-macaque group, which has spread widely through Asia and Africa and a variety of habitats. Another is that the baboons are the largest of all the monkeys. A third reason is that they have a relatively great ground-living capability in a type of habitat, the savanna, that was probably crucial in the emergence of early man. These savanna-dwelling baboons spend much more time in open country at a distance from trees than the chimps do. Based mainly on the extensive field work of Irven Devore (Harvard), the late K. R. L. Hall, Sherwood Washburn, and Tim Ransom (Berkeley), plus our own observations, we can summarize the conditions under which baboon threat and attack patterns are likely to occur:

1. Protection of the troop by adult males against predators, such as lions and cheetahs.
2. Protection of infants, both by their mothers and by adult males.
3. Resolution of severe fighting within the troop by adult males.
4. Formation and maintenance of consort pairs at the peak of estrus.
5. Attainment of preferred sleeping sites in the trees, particularly in the presence of predators.
6. Acquisition of premium foods, such as figs, nuts, and bananas, especially when these foods are spatially concentrated rather than widely distributed.
7. Dominance interactions, especially in the presence of premium food, or scarcity of sleeping sites, or females in full estrus.
8. Exploration of strange or manifestly dangerous areas, which is a function largely of adult males.
9. Contact between different troops, especially if such contact is infrequent.

Even after a very tense, agonistic morning, these animals, with a whole valley to choose from, seek each other for an afternoon rest.

The baboons' habitat has tall grass in which predators can readily hide, so the problem of predator pressure is very different there than it is in the forest habitat.

To observe the baboons, we followed a troop of 42 animals of both sexes and all ages, who have spent their lifetimes together. It's largely a closed social system, but there is some transfer of males between troops.

At one point the troop met with a lioness hunting. When she appeared, 39 of the 42 animals broke for the nearest trees—about a half mile away—while three adult males stood their ground. And so, in a moment, there was a phalanx of adult males flashing those impressive canine teeth interposed between the lioness and the rest of the troop. This is a case where social organization clearly meets a survival requirement.

Most of the threat and attack behavior on the part of the female is elicited by some kind of interference with her infant; but both males and females will very stoutly defend an infant, especially if the infant is giving a distress call.

The two most dominant males in the troop, Alpha and Beta, rarely got into real fighting. Ordinarily they stayed 100 yards apart at opposite ends of the troop. Their only serious quarrels arose over premium foods.

An older infant we called Torn Ear spent much of his day observing Alpha, and he enjoyed Alpha's protection. Torn Ear was perfectly free to threaten much larger baboons with impunity as long as Alpha was nearby. Torn

Ear was also much bolder about approaching us than any other infant, again with Alpha nearby. He observed, he imitated, and he often practiced what he imitated of Alpha's behavior. This observational learning in a social context seems to be the principal mode of learning for the nonhuman primates.

Since various biological indices suggest a rather close relation of man with chimpanzee and gorilla, it is interesting to note several patterns of aggression that are especially prominent in one or both of these species. We mention three.

First, both chimp and gorilla show more elaborate aggressive displays than any other primate species. This rich repertoire of threatening actions might well be called intimidation display. Patterns of submission and reassurance also seem to be more elaborate in these species than in other primates, and more similar to those of man.

Second, in chimpanzees, technology (if I may call it that) is more advanced than anything observed elsewhere among nonhuman primates. Simple tools are made according to an established tradition and are used effectively. Both spherical and cylindrical naturally occurring objects are used in threat and attack, sometimes with considerable efficacy.

Third, attachments based on kinship strongly influence behavior over a large part of the chimp's life, quite possibly all of it. Among other influences, kinship attachments may well serve to increase threat directed toward animals that are not part of the kinship subgroup, and also protection of the offspring's aggressive ventures in early life by the mother and probably by older siblings as well.

Grooming is an important pattern for limiting aggression. Whatever other hygienic functions it may have, it seems to have some kind of tension-relieving effect. This grooming session is between two high-ranking males, and is taking place during prolonged tension involving bananas.

Research workers in the field of bird and rodent behavior have studied various environmental conditions that elicit threat and attack patterns. Among them is the crowding of strangers, especially in the presence of valued resources such as food, sex, or nesting locations.

Is this also true of primates? Does the conjunction of these three conditions become an especially powerful instigation to aggression? Our observations of chimps and baboons leads us tentatively to answer yes to these questions, supporting the recent observations of other workers who have conducted studies of primates in natural habitats and in seminatural settings and laboratory experiments.

At Holloman Air Force Base in New Mexico, the Wilsons have observed chimps in a desert compound. When an animal was taken out of the group for a few days, even though he was quite well integrated into it earlier, he was very likely to be attacked when he was put back.

At Stanford, Patricia Barchas has been studying aggression in newly formed rhesus-macaque monkey groups. She finds that fighting is most likely to occur in the first few minutes of their contact with each other, as the strangers are introduced, and then later when food is made available under these crowded conditions.

Southwick, working in Calcutta, has established base-line frequencies for each of 20 behaviors occurring in a

Among baboons and a variety of other species, stable, established groups tend to avoid each other, and there is a good deal of tension when they meet.

social group of 17 rhesus-macaque monkeys composed of adults, juveniles, and yearlings of both sexes. After the group had stabilized, new animals were introduced from time to time in the 25- by 40-foot enclosure. New juveniles were mainly attacked by the resident juveniles; adult females were most likely to be attacked by resident females; and new adult males were attacked mainly by the adult males. For each class of introduced animals, it was found that the class whose status was threatened most directly was most active in the aggressive responses to the stranger.

Southwick also reduced the space by half to determine if crowding alone, in a familiar setting, increases fighting. It did, but modestly. At least under the conditions he used, the introduction of strangers was a more potent instigation to fighting than crowding, although both had some effect.

Generally speaking, among the baboons and a variety of other species, stable, established groups in nature tend to avoid each other, and there is a good deal of tension when they meet. However, it has recently been found in the monkey islands off Puerto Rico that some males fight their way into other groups, then later—even years later—may help a younger brother to enter that group.

Also from the Puerto Rican monkey islands comes evidence that the size of a monkey group is correlated with its dominance. In general, the smaller groups give way to larger ones. If the disparity is great, there is not likely to be more fighting, unless the resources available to them are very condensed and crowded.

Are there any general aggressive patterns common to primate species that are relatively closely related to man? We can make a tentative list of such patterns, referring not to the threat and attack patterns per se, but rather to the conditions under which they most commonly occur:

1. Dominance-submission transactions
2. The redirection of aggression downward in the dominance hierarchy
3. The protection of infants
4. When sought-after resources are in concentrated or short supply—for example, premium food, or a female at the peak of estrus
5. The meeting of relatively unfamiliar animals—which may be individuals, subgroups of an established group, or intergroup contact
6. Defense against predators
7. Killing and eating young animals of other species
8. Terminating severe disputes among subordinate animals

Factors of this sort may well have given selective advantage to aggressive primates over millions of years, providing they could regulate their aggressive behavior. Until now most of the research has focused on the sources and instigation of aggressive behavior; future work will profit from paying as much attention to the regulation and control of aggressive tendencies.

Hormonal influences upon brain organization early in life have been shown to affect later aggressive and sexual behavior. The pioneering work in the area was done with rodents. For example, brief treatment of newborn female rats with testosterone results in a lifelong abolition of female sex behavior and a tendency toward male patterns of aggressive behavior as well. That work was later extended by Young, Goy, and Phoenix to rhesus-macaque monkeys. He gave testosterone in large doses to pregnant monkeys; if the pregnant monkey was carrying a female in utero, that female was to some extent masculinized by the testosterone, both in some anatomical and in some behavioral characteristics—for example, clitoral enlargement.

The females who had been androgenized by testosterone in utero were shifted in a male-like direction: They initiated play more often, then engaged in rough-and-tumble play more often, and they threatened other animals more often than females who had not been exposed to androgens in utero.

Eight such monkeys have been followed into adult life at the Oregon Primate Center in Beaverton. These eight animals show a good deal of threatening behavior as adults, although some other measures of aggression have declined over the years under the laboratory conditions that were employed.

It is plausible that processes of this kind may have continued to operate through the long course of human evolution. But because of the extraordinary learning capacities characteristic of our species, it seems unlikely that the early exposure of brain cells to male sex hormone would establish a fixed complex response pattern for a lifetime. It seems more likely that some general orientation would be influenced by the early male hormone so that aggressive patterns are in some way attractive and readily learned.

Is there any evidence at all of similar effects in human development? John Money and his colleagues at Johns Hopkins studied more than 20 girls who had been exposed

When the baboon threatens, whether for aggressive or defensive purposes, he displays impressive canine teeth.

to various androgens in utero. They differ from a non-androgenized control group in several respects. The androgenized girls tend to be described by themselves and others as tomboys; they prefer outdoor sports requiring a great deal of energy and vigor, prefer rough play, and prefer toys ordinarily chosen by boys, such as guns. These observations raise an important question and illustrate how a lot of inquiry from basic research on the biology of sex differentiation applies to an important human problem.

But surely the hormone does not act on some template for guns somewhere in the brain. How, then, could such an effect be achieved?

Recall the emphasis on observational learning in the social environment for nonhuman primates. It may be that if the attention of the young primate is drawn to one sex even somewhat preferentially over another, then a great deal of learning will follow from it, such as what kind of objects are characteristically used by members of that sex.

In nonhuman primates, and maybe in human infants and young children, we might learn something from experimental methods for analyzing the deployment of attention. It is feasible to expose isolation-reared monkeys to different kinds of stimuli to see if they prefer to look at certain kinds of stimuli rather than others. I predict, for instance, that if we gave an isolation-reared monkey the

Several of the recent field studies of primates have shown striking behavioral changes at adolescence, which presumably depend, at least in part, on the hormonal changes in the males.

chance to look at various pictures, which included rough-and-tumble play, that males would spend more time looking at rough-and-tumble play at some stage in their early development than females would. In any case, that is testable.

Something similar to that has been done by Sackett in Harry Harlow's Wisconsin laboratory. His experimental setup consisted of isolation-rearing for nine months, during which he showed the monkeys various pictures. The pictures included both monkey and non-monkey stimuli. The first point of interest is that they spend much more time in infancy looking at the monkey stimuli than non-monkey stimuli, including pictures of people. Within the monkey stimuli, one finding is particularly interesting in the context of this discussion. A full-face threat elicited a peculiarly strong response—vocalizations and what is described as emotional disturbance. The response to the full-face threat was particularly strong between two and a half and four months of age. Something about that stimulus complex elicits a very strong, emotionally charged response in the isolation-reared monkey. So it is not difficult to imagine how an infant, once his attention has been drawn powerfully to a certain kind of behavior, would go on to learn a great deal about it.

What can we say about the role of the early social environment in shaping the development of aggressive behavior? I have touched on it already, and Harry Harlow presented some relevant material in the preceding article. The isolation-reared animals that he talked about are generally highly fearful and prone to outbursts of violence. Also, the infants who experienced brutality from their motherless mothers were themselves significantly more aggressive during the eight months they were studied than were the infants raised by normal mothers.

Lately the isolation-reared primates have been followed to see what happens several years later—at puberty, adolescence, and adulthood. In at least some of the work coming out of the Wisconsin laboratories, it looks as if the aggressiveness does not spontaneously decline with the passage of years after the monkeys are brought out of isolation. Indeed, for some the aberrant behavior becomes more pronounced later in life. Perhaps the onset of puberty is partially responsible for this later exacerbation in males. It may be no coincidence that the onset of puberty in males is associated with a sharp rise in circulating testosterone levels and with heightened aggressiveness. Several of the recent field studies of primate species have shown striking behavioral changes at adolescence, which presumably depend, at least in part, on the hormonal changes in the males.

Lately developmental psychologists have been calling attention to the importance of observational learning in young children. The child between one and two years of age is a devoted watcher; observation and imitation may well be the principal modes of learning at that age. If the primate ethological studies are going to have a stimulating impact on human research, I think it would be particularly on studies of infancy and early childhood. In fact, McGraw in Edinburgh recently published a study of young children in which he applied quite directly the agonistic categories from field studies of nonhuman primates and found they worked quite well.

There is also the major line of inquiry that Bandura and his colleagues have conducted at Stanford over some years with three- to five-year-old children on susceptibility of children to learning aggressive patterns by viewing models who act aggressively. For example, in one experiment preschool children were exposed to a model attacking a target for only ten minutes in a laboratory situation; a control group experienced the same situation without an aggressive model. When the children were tested in the same situation six months later, those who had witnessed the attack were much more aggressive toward the target object than were the others. A ten-minute exposure enhanced physical aggressiveness in the same situation six months later.

In general, biological predispositions to learning aggressive patterns and exposure to specific social learning situations may interact to produce great individual differences in aggressiveness during later life. In analyzing such problems, the effective conjunction of biological and psychosocial disciplines, so far rarely achieved, holds much promise for future understanding. It hardly seems necessary to point out the aggressive tendencies of the human species today. Whatever adaptive functions such behavior may have served in man's evolutionary past, there is serious question about its utility in contemporary society. The risks inherent in such behavior have been greatly amplified within our own lifetime, and yet these problems at present attract only a modest amount of attention in the scientific community. It is difficult to imagine a more important area for research in the future. Let us hope that the biological and behavioral sciences in the next decade will really pursue these problems, which are so poignant in their human impact, so urgently in need of solution, and so pertinent to the concerns of our time.