



BONOBO

Sex & Society

BY FRANS B. M. DE WAAL

The behavior of a close relative challenges assumptions about male supremacy in human evolution

At a juncture in history during which women are seeking equality with men, science arrives with a belated gift to the feminist movement. Male-biased evolutionary scenarios—Man the Hunter, Man the Toolmaker and so on—are being challenged by the discovery that females play a central, perhaps even dominant, role in the social life of one of our nearest relatives. In the past two decades many strands of knowledge have come together concerning a relatively unknown ape with an unorthodox repertoire of behavior: the bonobo.

The bonobo is one of the last large mammals to be found by science. The creature was discovered in 1929 in a Belgian colonial museum, far from its lush African habitat. A German anatomist, Ernst Schwarz, was scrutinizing a skull that had been ascribed to a juvenile chimpanzee because of its small size, when he realized that it belonged to an adult. Schwarz declared that he had stumbled on a new subspecies of chimpanzee. But soon the animal was assigned the status of an entirely distinct species within the same genus as the chimpanzee, *Pan*.

The bonobo was officially classified as *Pan paniscus*, or the diminutive *Pan*. But I believe a different label might have been selected had the discoverers known then what we know now. The old taxonomic name of the chimpanzee, *P. satyrus*—which refers to the myth of apes as lustful satyrs—would have been perfect for the bonobo.

The species is best characterized as female-centered and egalitarian and as one that substitutes sex for aggression. Whereas in most other species sexual behavior is a fairly distinct category, in the bonobo it is part and parcel of social

BONOBO FEMALE interacts with an infant. Juvenile bonobos depend on their mothers for milk and transport for up to five years. They are extremely well tolerated by adults, who have rarely been seen to attack or threaten them.

relations—and not just between males and females. Bonobos engage in sex in virtually every partner combination (although such contact among close family members may be suppressed). And sexual interactions occur more often among bonobos than among other primates. Despite the frequency of sex, the bonobo's rate of reproduction in the wild is about the same as that of the chimpanzee. A female gives birth to a single infant at intervals of between five and six years. So bonobos share at least one very important characteristic with our own species, namely, a partial separation between sex and reproduction.

A Near Relative

THIS FINDING commands attention because the bonobo shares more than 98 percent of our genetic profile, making it as close to a human as, say, a fox is to a dog. The split between the human line of ancestry and the line of the chimpanzee and the bonobo is believed to have occurred a mere eight million years ago. The subsequent divergence of the chimpanzee and the bonobo lines came much later, perhaps prompted by the chimpanzee's need to adapt to relatively open, dry habitats.

In contrast, bonobos probably never left the protection of the trees. Their present range lies in humid forests south of the Congo River, where perhaps fewer than 10,000 bonobos survive. (Given the species' slow rate of reproduction, the rapid destruction of its tropical habitat and the political instability of central Africa, there is reason for much concern about its future.)

If this evolutionary scenario of ecological continuity is true, the bonobo may have undergone less transformation than either humans or chimpanzees. It could most closely resemble the common ancestor of all three modern species. Indeed, in the 1930s Harold J. Coolidge—the American anatomist who gave the bonobo its eventual taxonomic status—suggested that the ani-

mal might be most similar to the primate, because its anatomy is less specialized than is the chimpanzee's. Bonobo body proportions have been compared with those of the australopithecines, a form of prehuman. When the apes stand or walk upright, they look as if they stepped straight out of an artist's impression of early hominids.

Not too long ago the savanna baboon was regarded as the best living model of the human ancestor. That primate is adapted to the kinds of ecological conditions that prehumans may have faced after descending from the trees. But in the late 1970s chimpanzees, which are much more closely related to humans, became the model of choice. Traits that are observed in chimpanzees—including cooperative hunting, food sharing, tool use, power politics and primitive warfare—were absent or not as developed in baboons. In the laboratory the apes have been able to learn sign language and to recognize themselves in a mirror, a sign of self-awareness not yet demonstrated in monkeys.

Although selecting the chimpanzee as the touchstone of hominid evolution represented a great improvement, at least one aspect of the former model did not need to be revised: male superiority remained the natural state of affairs. In both baboons and chimpanzees, males are conspicuously dominant over females; they reign supremely and often brutally. It is highly unusual for a fully grown male chimpanzee to be dominated by any female.

Enter the bonobo. Despite their common name—the pygmy chimpanzee—bonobos cannot be distinguished from the chimpanzee by size. Adult males of the smallest subspecies of chimpanzee weigh some 43 kilograms (95 pounds) and females 33 kilograms (73 pounds), about the same as bonobos. Although female bonobos are much smaller than the males, they seem to rule.

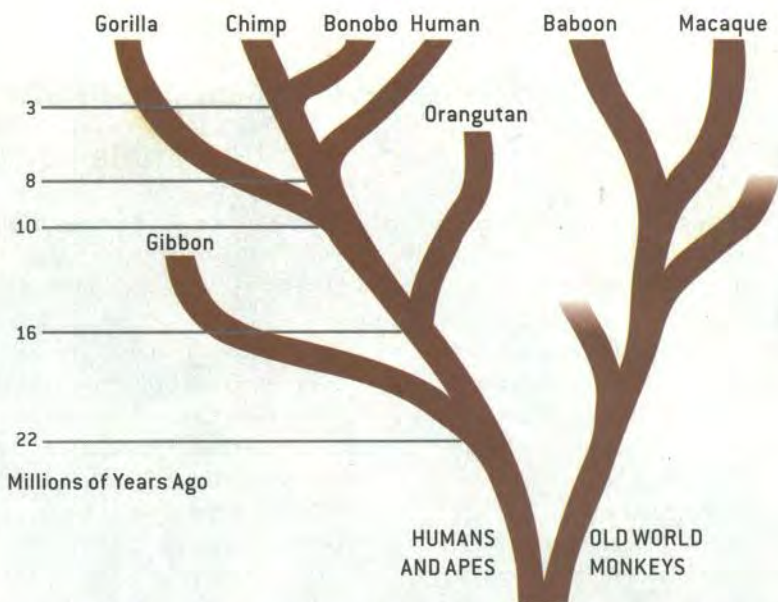
Graceful Apes

IN PHYSIQUE, a bonobo is as different from a chimpanzee as a Concorde is from a Boeing 747. I do not wish to offend any chimpanzees, but bonobos have more style. The bonobo, with its long legs and small head atop narrow shoulders, has a more gracile build than does a chimpanzee. Bonobo lips are reddish in a black face, the ears small and the nostrils almost as wide as a gorilla's. These primates also have a flatter, more open face with a higher forehead than the chimpanzee's and—to top it all off—an attractive coiffure with long, fine, black hair neatly parted in the middle.

Like chimpanzees, female bonobos nurse and carry around their young for up to five years. By the age of seven the offspring reach adolescence. Wild females give birth for the first time at 13 or 14 years of age, becoming full grown by about 15. A bonobo's longevity is unknown, but judging by the chimpanzee it may be older than 40 in the wild and close to 60 in captivity.

Fruit is central to the diets of both wild bonobos and chimpanzees. The former supplement with more pith from herbaceous plants, and the latter add meat. Although bonobos do eat invertebrates and occasionally capture and eat small vertebrates, including mammals, their diet seems to contain relatively little animal protein. Unlike chimpanzees, they have not been observed to hunt monkeys.

Whereas chimpanzees use a rich array of strategies to obtain foods—from cracking nuts with stone tools to fishing for ants and termites with sticks—tool use in wild bonobos seems undeveloped. (Captive bonobos use tools skillfully.) Apparently as intelligent as chimpanzees, bonobos have, however, a far more sensitive temperament. During World War II bombing of Hellabrunn, Germany, the bonobos in a near-



EVOLUTIONARY TREE of primates, based on DNA analysis, shows that humans diverged from bonobos and chimpanzees a mere eight million years ago. The three species share more than 98 percent of their genetic makeup.

by zoo all died of fright from the noise; the chimpanzees were unaffected.

Bonobos are also imaginative in play. I have watched captive bonobos engage in "blindman's buff." A bonobo covers her eyes with a banana leaf or an arm or by sticking two fingers in her eyes. Thus handicapped, she stumbles around on a climbing frame, bumping into others or almost falling. She seems to be imposing a rule on herself: "I cannot look until I lose my balance." Other apes and monkeys also indulge in this game, but I have never seen it performed with such dedication and concentration as by bonobos.

Juvenile bonobos are incurably playful and like to make funny faces, sometimes in long solitary pantomimes and at other times while tickling one another. Bonobos are, however, more controlled in expressing their emotions—whether it be joy, sorrow, excitement or anger—than are the extroverted chimpanzees. Male chimpanzees often engage in spectacular charging displays in which they show off their strength: throwing rocks, breaking

branches and uprooting small trees in the process. They keep up these noisy performances for many minutes, during which most other members of the group wisely stay out of their way. Male bonobos, on the other hand, usually limit displays to a brief run while dragging a few branches behind them.

Both primates signal emotions and intentions through facial expressions and hand gestures, many of which are also present in the nonverbal communication of humans. For example, bonobos will beg by stretching out an open hand (or, sometimes, a foot) to a possessor of food and will pout their lips and make whimpering sounds if the effort is unsuccessful. But bonobos make different sounds than chimpanzees do. The renowned low-pitched, extended "huuu-huuu" pant-hooting of the latter contrasts with the rather sharp, high-pitched barking sounds of the bonobo.

Love, Not War

MY OWN INTEREST in bonobos came not from an inherent fascination with their charms but from research on aggressive behavior in primates. I was particularly intrigued with the aftermath of conflict. After two chimpanzees have fought, for instance, they may come together for a hug and mouth-to-mouth kiss. Assuming that such reunions serve to restore peace and har-

mony, I labeled them reconciliations.

Any species that combines close bonds with a potential for conflict needs such conciliatory mechanisms. Thinking how much faster marriages would break up if people had no way of compensating for hurting one another, I set out to investigate such mechanisms in several primates, including bonobos. Although I expected to see peacemaking in these apes, too, I was little prepared for the form it would take.

For my study, which began in 1983, I chose the San Diego Zoo. At the time, it housed the world's largest captive bonobo colony—10 members divided into three groups. I spent entire days in front

of the enclosure with a video camera, which was switched on at feeding time. As soon as a caretaker approached the enclosure with food, the males would develop erections. Even before the food was thrown into the area, the bonobos would be inviting each other for sex: males would invite females, and females would invite males and other females.

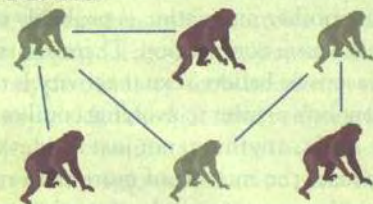
Sex, it turned out, is the key to the social life of the bonobo. The first suggestion that the sexual behavior of bonobos is different had come from observations at European zoos. Wrapping their findings in Latin, primatologists Eduard Tratz and Heinz Heck reported in 1954 that the chimpanzees at Hel-

labrunn mated *more canum* (like dogs) and bonobos *more hominum* (like people). In those days, face-to-face copulation was considered uniquely human, a cultural innovation that needed to be taught to preliterate people (hence the term "missionary position"). These early studies, written in German, were ignored by the international scientific establishment. The bonobo's human-like sexuality needed to be rediscovered in the 1970s before it became accepted as characteristic of the species.

Bonobos become sexually aroused remarkably easily, and they express this excitement in a variety of mounting positions and genital contacts. Al-

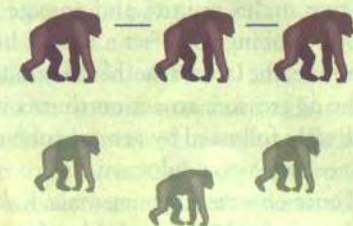
SOCIAL ORGANIZATION AMONG VARIOUS PRIMATES

BONOBO



Bonobo communities are peace-loving and generally egalitarian. The strongest social bonds (blue lines) are those among females (green), although females also bond with males. The status of a male (gray) depends on the position of his mother, to whom he remains closely bonded for her entire life.

CHIMPANZEE



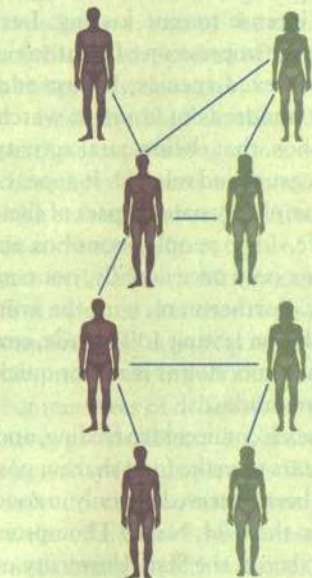
In chimpanzee groups the strongest bonds are established between the males in order to hunt and to protect their shared territory. The females live in overlapping home ranges within this territory but are not strongly bonded to other females or to any one male.

GIBBON



Gibbons establish monogamous, egalitarian relations, and one couple will maintain a territory to the exclusion of other pairs.

HUMAN



Human society is the most diverse among the primates. Males unite for cooperative ventures, whereas females also bond with those of their own sex. Monogamy, polygamy and polyandry are all in evidence.

GORILLA



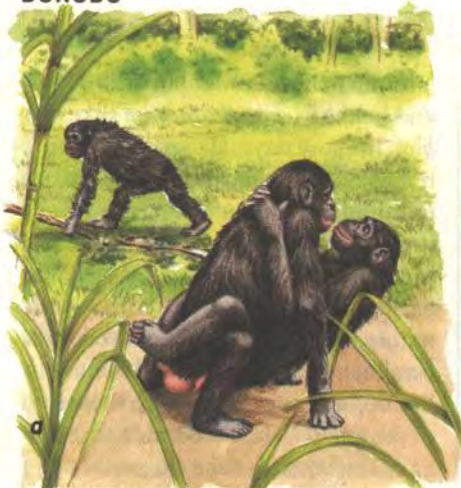
The social organization of gorillas provides a clear example of polygamy. Usually a single male maintains a range for his family unit, which contains several females. The strongest bonds are those between the male and his females.

ORANGUTAN



Orangutans live solitary lives with little bonding in evidence. Male orangutans are intolerant of one another. In his prime, a single male establishes a large territory, within which live several females. Each female has her own, separate home range.

BONOBO



DOMINANCE BY BONDING is evinced by female bonobos, who engage in genito-genital (GG) rubbing before eating sugarcane (a), while a bigger male displays to no avail. The females then share the food without competition (b). Only when they leave can the male get to the sugarcane (c). In male-dominated chimpanzee society the male eats first (d), while the females wait at a safe distance. After he leaves (e), carrying as many bananas as he can, the dominant female gets what is left (f). Small amounts of sugarcane and bananas are provided at some research sites in the Democratic Republic of the Congo (formerly Zaire).

though chimpanzees virtually never adopt face-to-face positions, bonobos do so in one out of three copulations in the wild. Furthermore, the frontal orientation of the bonobo vulva and clitoris strongly suggest that the female genitalia are adapted for this position.

Another similarity with humans is increased female sexual receptivity. The tumescent phase of the female's genitals, resulting in a pink swelling that signals willingness to mate, covers a much longer part of estrus in bonobos than in chimpanzees. Instead of a few days out of her cycle, the female bonobo is almost continuously sexually attractive and active [see illustration on page 20].

Perhaps the bonobo's most typical sexual pattern, undocumented in any other primate, is genito-genital rubbing (or GG rubbing) between adult females. One female facing another clings with arms and legs to a partner that, standing on both hands and feet, lifts her off the ground. The two females then rub their genital swellings laterally together, emitting grins and squeals that probably reflect orgasmic experiences. (Laboratory experiments on stump-tailed macaques have demonstrated that women are not the only female primates capable of physiological orgasm.)

Male bonobos, too, may engage in pseudocopulation but generally per-

form a variation. Standing back to back, one male briefly rubs his scrotum against the buttocks of another. They also practice so-called penis-fencing, in which two males hang face to face from a branch while rubbing their erect penises together.

The diversity of erotic contacts in bonobos includes sporadic oral sex, massage of another individual's genitals and intense tongue-kissing. Lest this leave the impression of a pathologically oversexed species, I must add, based on hundreds of hours of watching bonobos, that their sexual activity is rather casual and relaxed. It appears to be a completely natural part of their group life. Like people, bonobos engage in sex only occasionally, not continuously. Furthermore, with the average copulation lasting 13 seconds, sexual contact in bonobos is rather quick by human standards.

That sex is connected to feeding, and even appears to make food sharing possible, has been observed not only in zoos but also in the wild. Nancy Thompson-Handler, then at the State University of New York at Stony Brook, saw bonobos in the Lomako Forest of the Democratic Republic of the Congo (formerly Zaire) engage in sex after they had entered trees loaded with ripe figs or when one among them had captured a prey ani-

mal, such as a small forest duiker. The flurry of sexual contacts would last for five to 10 minutes, after which the apes would settle down to consume the food.

One explanation for the sexual activity at feeding time could be that excitement over food translates into sexual arousal. This idea may be partly true. Yet another motivation is probably the real cause: competition. There are two reasons to believe sexual activity is the bonobo's answer to avoiding conflict.

First, anything, not just food, that arouses the interest of more than one bonobo at a time tends to result in sexual contact. If two bonobos approach a cardboard box thrown into their enclosure, they will briefly mount each other before playing with the box. Such situations lead to squabbles in most other species. But bonobos are quite tolerant, perhaps because they use sex to divert attention and to diffuse tension.

Second, bonobo sex often occurs in aggressive contexts totally unrelated to food. A jealous male might chase another away from a female, after which the two males reunite and engage in scrotal rubbing. Or after a female hits a juvenile, the latter's mother may lunge at the aggressor, an action that is immediately followed by genital rubbing between the two adults.

I once observed a young male, Kako, inadvertently blocking an older, female juvenile, Leslie, from moving along a branch. First, Leslie pushed him; Kako, who was not very confident in trees, tightened his grip, grinning nervously. Next Leslie gnawed on one of his hands, presumably to loosen his grasp. Kako ut-

CHIMPANZEE



tered a sharp peep and stayed put. Then Leslie rubbed her vulva against his shoulder. This gesture calmed Kako, and he moved along the branch. It seemed that Leslie had been very close to using force but instead had reassured both herself and Kako with sexual contact.

During reconciliations, bonobos use the same sexual repertoire as they do during feeding time. Based on an analysis of many such incidents, my study yielded the first solid evidence for sexual behavior as a mechanism to overcome aggression. Not that this function is absent in other animals—or in humans, for that matter—but the art of sexual reconciliation may well have reached its evolutionary peak in the bonobo. For these animals, sexual behavior is indistinguishable from social behavior. Given its peacemaking and appeasement functions, it is not surprising that sex among bonobos occurs in so many different partner combinations, including between juveniles and adults. The need for peaceful coexistence is obviously not restricted to adult heterosexual pairs.

Female Alliance

APART FROM maintaining harmony, sex is also involved in creating the singular social structure of the bonobo. This use of sex becomes clear when studying bonobos in the wild. Field research on bonobos started only in the mid-1970s, a decade after the most important studies on wild chimpanzees had been initiated. In terms of continuity and invested (wo)manpower, the chimpanzee projects of Jane Goodall and Toshisada

Nishida, both in Tanzania, are unparalleled. But bonobo research by Takayoshi Kano and others of Kyoto University began to show the same payoffs after two decades at Wamba in the Democratic Republic of the Congo.

Both bonobos and chimpanzees live in so-called fission-fusion societies. The apes move alone or in small parties of a few individuals at a time, the composition of which changes constantly. Several bonobos traveling together in the morning might meet another group in the forest, whereupon one individual from the first group wanders off with others from the second group, while those left behind forage together. All associations, except the one between mother and dependent offspring, are of a temporary character.

Initially this flexibility baffled investigators, making them wonder if these apes formed any social groups with stable membership. After years of documenting the travels of chimpanzees in the Mahale Mountains, Nishida first reported that they form large communities: all members of one community mix freely in ever changing parties, but members of different communities never gather. Later, Goodall added territoriality to this picture. That is, not only do communities not mix, but males of different chimpanzee communities engage in lethal battles.

In both bonobos and chimpanzees, males stay in their natal group, whereas females tend to migrate during adolescence. As a result, the senior males of a chimpanzee or bonobo group have known all junior males since birth, and

all junior males have grown up together. Females, on the other hand, transfer to an unfamiliar and often hostile group where they may know no one. A chief difference between chimpanzee and bonobo societies is the way in which young females integrate into their new community.

On arrival in another community, young bonobo females at Wamba single out one or two senior resident females for special attention, using frequent GG rubbing and grooming to establish a relation. If the residents reciprocate, close associations are set up, and the younger female gradually becomes accepted into the group. After producing her first offspring, the young female's position becomes more stable and central. Eventually the cycle repeats with younger immigrants, in turn, seeking a good relation with the now established female. Sex thus smooths the migrant's entrance into the community of females, which is much more close-knit in the bonobo than in the chimpanzee.

Bonobo males remain attached to their mothers all their lives, following them through the forest and being dependent on them for protection in aggressive encounters with other males. As a result, the highest-ranking males of a bonobo community tend to be sons of important females.

What a contrast with chimpanzees! Male chimpanzees fight their own battles, often relying on the support of other males. Furthermore, adult male chimpanzees travel together in same-sex parties, grooming one another fre-

quently. Males form a distinct social hierarchy with high levels of both competition and association. Given the need to stick together against males of neighboring communities, their bonding is not surprising: failure to form a united front might result in the loss of lives and territory. The danger of being male is reflected in the adult sex ratio of chimpanzee populations, with considerably fewer males than females.

Serious conflict between bonobo groups has been witnessed in the field, but it seems quite rare. On the contrary, reports exist of peaceable mingling, including mutual sex and grooming, between what appear to be different communities. If intergroup combat is indeed unusual, it may explain the lower rate of all-male associations. Rather than being male-bonded, bonobo society gives the impression of being female-bonded, with even adult males relying on their mothers instead of on other males. No wonder Kano calls mothers the "core" of bonobo society.

The bonding among female bonobos violates a fairly general rule, outlined by Harvard University anthropologist Richard W. Wrangham, that the sex that stays in the natal group develops the strongest mutual bonds. Bonding among male chimpanzees follows naturally because they remain in the community of their birth. The same is true for female kinship bonding in Old World monkeys, such as macaques and baboons,

where males are the migratory sex.

Bonobos are unique in that the migratory sex, females, strongly bond with same-sex strangers later in life. In setting up an artificial sisterhood, bonobos can be said to be secondarily bonded. (Kinship bonds are said to be primary.) Although we now know *how* this happens—through the use of sexual contact and grooming—we do not yet know *why* bonobos and chimpanzees differ in this respect. The answer may lie in the different ecological environments of bonobos and chimpanzees—such as the abundance and quality of food in the forest. But it is uncertain if such explanations will suffice.

Bonobo society is, however, not only female-centered but also appears to be female-dominated. Bonobo specialists, while long suspecting such a reality, had been reluctant to make the controversial claim. But in 1992, at the 14th Congress of the International Primatological Society in Strasbourg, investigators of both captive and wild bonobos presented data that left little doubt about the issue.

Amy R. Parish of the University of California, Davis, reported on food competition in identical groups (one adult male and two adult females) of chimpanzees and bonobos at the Stuttgart Zoo. Honey was provided in a "termite hill" from which it could be extracted by dipping sticks into a small hole. As soon as honey was made avail-

able, the male chimpanzee would make a charging display through the enclosure and claim everything for himself. Only when his appetite was satisfied would he let the females fish for honey.

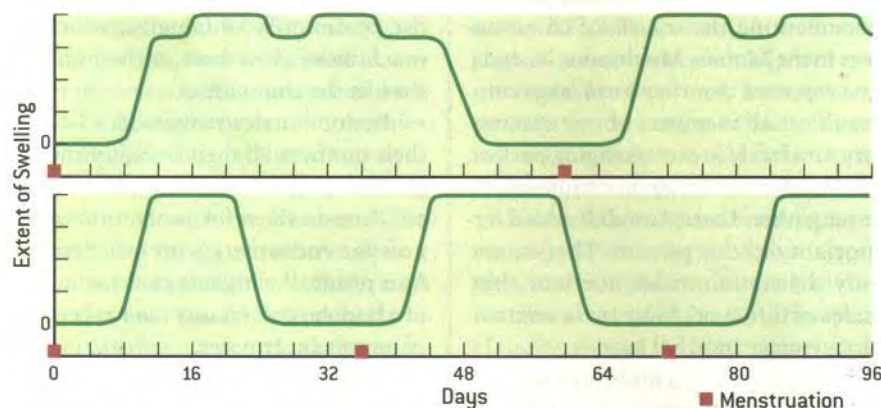
In the bonobo group, it was the females that approached the honey first. After having engaged in some GG rubbing, they would feed together, taking turns with virtually no competition between them. The male might make as many charging displays as he wanted; the females were not intimidated and ignored the commotion.

Observers at the Belgian animal park of Planckendael, which currently has the most naturalistic bonobo colony, reported similar findings. If a male bonobo tried to harass a female, all females would band together to chase him off. Because females appeared more successful in dominating males when they were together than on their own, their close association and frequent genital rubbing may represent an alliance. Females may bond so as to outcompete members of the individually stronger sex.

The fact that they manage to do so not only in captivity is evident from zoologist Takeshi Furuichi's summary of the relation between the sexes at Wamba, where bonobos are enticed out of the forest with sugarcane. "Males usually appeared at the feeding site first, but they surrendered preferred positions when the females appeared. It seemed that males appeared first not because they were dominant, but because they had to feed before the arrival of females," Furuichi reported at Strasbourg.

Sex for Food

OCCASIONALLY, the role of sex in relation to food is taken one step further, bringing bonobos very close to humans in their behavior. It has been speculated by anthropologists—including C. Owen Lovejoy of Kent State University and Helen Fisher of Rutgers University—that sex is partially separated from reproduction in our species because it serves to cement mutually profitable relationships between men and women. The human female's capacity to mate throughout her cycle and her strong sex drive



FEMALE RECEPTIVITY for sex, manifested by swollen genitals, occupies a much larger proportion of the estrus cycle of bonobos (top) than of chimpanzees (bottom). The receptivity of bonobos continues through lactation. [In chimpanzees, it disappears.] This circumstance allows sex to play a large part in the social relations of bonobos. The graph was provided by Jeremy Dahl of the Yerkes National Primate Research Center.



BEHAVIOR among bonobos is often reminiscent of that among humans. A female and an infant play (top left); a bonobo walks upright, using his hands to carry food (top right); two juveniles practice sex without penetration (bottom left); and a male and female have sex while facing each other (bottom right), a position once thought to be uniquely human.

allow her to exchange sex for male commitment and paternal care, thus giving rise to the nuclear family.

This arrangement is thought to be favored by natural selection because it allows women to raise more offspring than they could if they were on their own. Although bonobos clearly do not establish the exclusive heterosexual bonds characteristic of our species, their behavior does fit important elements of this model. A female bonobo shows extended receptivity and uses sex to obtain a male's favors when—usually because of youth—she is too low in social status to dominate him.

At the San Diego Zoo, I observed that if Loretta was in a sexually attractive state, she would not hesitate to approach the adult male, Vernon, if he had food. Presenting herself to Vernon, she would mate with him and make high-pitched food calls while taking over his entire bundle of branches and leaves. When Loretta had no genital swelling, she would wait until Vernon was ready

to share. Primatologist Suehisa Kuroda reports similar exchanges at Wamba: "A young female approached a male, who was eating sugarcane. They copulated in short order, whereupon she took one of the two canes held by him and left."

Despite such quid pro quo between the sexes, there are no indications that bonobos form humanlike nuclear families. The burden of raising offspring appears to rest entirely on the female's shoulders. In fact, nuclear families are probably incompatible with the diverse

use of sex found in bonobos. If our ancestors started out with a sex life similar to that of bonobos, the evolution of the family would have required dramatic change.

Human family life implies paternal investment, which is unlikely to develop unless males can be reasonably certain that they are caring for their own, not someone else's, offspring. Bonobo society lacks any such guarantee, but humans protect the integrity of their family units through all kinds of moral restrictions and taboos. Thus, although our species is characterized by an extraordinary interest in sex, there are no societies in which people engage in it at the drop of a hat (or a cardboard box, as the case may be). A sense of shame and a desire for domestic privacy are typical human concepts related to the evolution and cultural bolstering of the family.

Yet no degree of moralizing can make sex disappear from every realm of human life that does not relate to the nuclear family. The bonobo's behavioral peculiarities may help us understand the role of sex and may have serious implications for models of human society. Just imagine that we had never heard of chimpanzees or baboons and had known bonobos first. We would at present most likely believe that early hominids lived in female-centered societies, in which sex served important social functions and in which warfare was rare or absent. In the end, perhaps the most successful reconstruction of our past will be based not on chimpanzees or even on bonobos but on a three-way comparison of chimpanzees, bonobos and humans. ■

MORE TO EXPLORE

The Pygmy Chimpanzee: Evolutionary Biology and Behavior. Edited by Randall L. Susman. Plenum Press, 1984.

The Communicative Repertoire of Captive Bonobos (*Pan paniscus*) Compared to That of Chimpanzees. F.B.M. de Waal in *Behaviour*, Vol. 106, Nos. 3–4, pages 183–251; September 1988.

Understanding Chimpanzees. Edited by Paul Heltne and Linda A. Marquardt. Harvard University Press, 1989.

The Last Ape: Pygmy Chimpanzee Behavior and Ecology. Takayoshi Kano. Stanford University Press, 1992.

Chimpanzee Cultures. Richard Wrangham, W. C. McGrew, Frans B. M. de Waal and Paul Heltne. Harvard University Press, 1994.

Bonobo: The Forgotten Ape. Frans B. M. de Waal, with photographs by Frans Lanting. University of California Press, 1996.