

What Are Friends For?

Among East African baboons, friendship means companions, health, safety . . . and, sometimes, sex.

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Virgil, a burly adult male olive baboon, closely followed Zizi, a middle-aged female easily distinguished by her grizzled coat and square muzzle. On her rump Zizi sported a bright pink swelling, indicating that she was sexually receptive and probably fertile. Virgil's extreme attentiveness to Zizi suggested to me—and all rival males in the troop—that he was her current and exclusive mate.

Zizi, however, apparently had something else in mind. She broke away from Virgil, moved rapidly through the troop, and presented her alluring sexual swelling to one male after another. Before Virgil caught up with her, she had managed to announce her receptive condition to several of his rivals. When Virgil tried to grab her, Zizi screamed and dashed into the bushes with Virgil in hot pursuit. I heard sounds of chasing and fighting coming from the thicket. Moments later Zizi emerged from the bushes with an older male named Cyclops. They remained together for several days, copulating often. In Cyclops's presence, Zizi no longer approached or even glanced at other males.

Primatologists describe Zizi and other olive baboons (*Papio cynocephalus anubis*) as promiscuous, meaning that both males and females usually mate with several members of the opposite sex within a short period of time. Promiscuous mating behavior characterizes many of the larger, more familiar primates, including chimpanzees, rhesus macaques, and gray langurs, as well as olive, yellow, and chacma baboons, the three subspecies of savanna baboon. In colloquial usage, promiscuity often connotes wanton and random sex, and several early studies of primates supported this stereotype. However, after years of laboriously recording thousands of copulations under natural conditions, the Peeping Toms of primate fieldwork have shown that, even in promiscuous species, sexual pairings are far from random.

Some adult males, for example, typically copulate much more often than others. Primatologists have explained these differences in terms of competition: the most dominant males monopolize females and prevent lower-ranking rivals from mating. But exceptions are frequent. Among baboons, the exceptions often involve scruffy, older males who mate in full view of younger, more dominant rivals.

A clue to the reason for these puzzling exceptions emerged when primatologists began to question an implicit assumption of the dominance hypothesis—that females were merely passive objects of male competition. But what if females were active arbiters in this system? If females preferred some males over others and were able to express these preferences, then models of mating activity based on male dominance alone would be far too simple.

Once researchers recognized the possibility of female choice, evidence for it turned up in species after species. The story of Zizi, Virgil, and Cyclops is one of hundreds of examples of female primates rejecting the sexual advances of particular males and enthusiastically cooperating with others. But what is the basis for female choice? Why might they prefer some males over others?

This question guided my research on the Eburru Cliffs troop of olive baboons, named after one of their favorite sleeping sites, a sheer rocky outcrop rising several hundred feet above the floor of the Great Rift Valley, about 100 miles northwest of Nairobi, Kenya. The 120 members of Eburru Cliffs spent their days wandering through open grassland studded with occasional acacia thorn trees. Each night they retired to one of a dozen sets of cliffs that provided protection from nocturnal predators such as leopards.

Most previous studies of baboon sexuality had focused on females who, like Zizi, were at the peak of sexual receptivity. A female baboon does not mate when she is pregnant or lactating, a period of abstinence lasting about eighteen months. The female then goes into estrus, and for about two weeks out of every thirty-five-day cycle, she mates. Toward the end of this two-week period she may ovulate, but usually the female undergoes four or five estrous cycles before she conceives. During pregnancy, she once again resumes a chaste existence. As a result, the typical female baboon is sexually active for less than 10 percent of her adult life. I thought that by focusing on the other 90 percent, I might learn something new. In particular, I suspected that routine, day-to-day relationships between males and pregnant or lactating (nonestrous) females might provide clues to female mating preferences.

Nearly every day for sixteen months, I joined the Eburru Cliffs baboons at their sleeping cliffs at dawn and traveled several miles with them while they foraged for roots, seeds, grass, and occasionally, small prey items, such as baby gazelles or hares (see "Predatory Baboons of Kekokey," *Natural History*, March 1976). Like all savanna baboon troops, Eburru Cliffs functioned as a cohesive unit organized around a core of related females, all of whom were born in the troop. Unlike the females, male savanna baboons leave their natal troop to join another where they may remain for many years, so most of the Eburru Cliffs adult males were immigrants. Since membership in the troop remained relatively constant during the period of my study, I learned to identify each individual. I relied on differences in size, posture, gait, and especially, facial features. To the practiced observer, baboons look as different from one another as human beings do.

As soon as I could recognize individuals, I noticed that particular females tended to turn up near particular males again and again. I came to think of these pairs as friends. Friendship among animals is not a well-documented phenomenon, so to convince skeptical colleagues that baboon friendship was real, I needed to develop objective criteria for distinguishing friendly pairs.

I began by investigating grooming, the amiable simian habit of picking through a companion's fur to remove dead skin and ectoparasites (see "Little Things That Tick Off Baboons," *Natural History*, February 1984). Baboons spend much more time grooming than is necessary for hygiene, and previous research had indicated that it is a good measure of social bonds.

Although eighteen adult males lived in the troop, each non-estrous female performed most of her grooming with just one, two, or occasionally, three males. For example, of Zizi's twenty-four grooming bouts with males, Cyclops accounted for thirteen, and a second male, Sherlock, accounted for all the rest. Different females tended to favor different males as grooming partners.

Another measure of social bonds was simply who was observed near whom. When foraging, traveling, or resting, each pregnant or lactating female spent a lot of time near a few males and associated with the others no more often than expected by chance. When I compared the identities of favorite grooming partners and frequent companions, they overlapped almost completely. This enabled me to develop a formal definition of friendship: any male that scored high on both grooming and proximity measures was considered a friend.

Virtually all baboons made friends; only one female and three males who had most recently joined the troop lacked such companions. Out of more than 600 possible adult female-adult male pairs in the troop, however, only about one in ten qualified as friends; these really were special relationships.

Several factors seemed to influence which baboons paired up. In most cases, friends were unrelated to each other, since the male had immigrated from another troop. (Four friendships, however, involved a female and an adolescent son who had not yet emigrated. Unlike other friends, these related pairs never mated.) Older females tended to be friends with older males; younger females with younger males. I witnessed occasional May-December romances, usually involving older females and

young adult males. Adolescent males and females were strongly rule-bound, and with the exception of mother-son pairs, they formed friendships only with one another.

Regardless of age or dominance rank, most females had just one or two male friends. But among males, the number of female friends varied greatly from none to eight. Although high-ranking males enjoyed priority of access to food and sometimes mates, dominant males did not have more female friends than low-ranking males. Instead it was the older males who had lived in the troop for many years who had the most friends. When a male had several female friends, the females were often closely related to one another. Since female baboons spend a lot of time near their kin, it is probably easier for a male to maintain bonds with several related females at once.

When collecting data, I focused on one nonestrous female at a time and kept track of her every movement toward or away from any male; similarly, I noted every male who moved toward or away from her. Whenever the female and male moved close enough to exchange intimacies, I wrote down exactly what happened. When foraging together, friends tended to remain a few yards apart. Males more often wandered away from females than the reverse, and females, more often than males, closed the gap. The female behaved as if she wanted to keep the male within calling distance, in case she needed his protection. The male, however, was more likely to make approaches that brought them within actual touching distance. Often, he would plunk himself down right next to his friend and ask her to groom him by holding a pose with exaggerated stillness. The female sometimes responded by grooming, but more often, she exhibited the most reliable sign of true intimacy: she ignored her friend and simply continued whatever she was doing.

In sharp contrast, when a male who was not a friend moved close to a female, she dared not ignore him. She stopped whatever she was doing and held still, often glancing surreptitiously at the intruder. If he did not move away, she sometimes lifted her tail and presented her rump. When a female is not in estrus, this is a gesture of appeasement, not sexual enticement. Immediately after this respectful acknowledgement of his presence, the female would slip away. But such tense interactions with nonfriend males were rare, because females usually moved away before the males came too close.

These observations suggest that females were afraid of most of the males in their troop, which is not surprising: male baboons are twice the size of females, and their canines are longer and sharper than those of a lion. All Eburru Cliffs males directed both mild and severe aggression toward females. Mild aggression, which usually involved threats and chases but no body contact, occurred most often during feeding competition or when the male redirected aggression toward a female after losing a fight with another male. Females and juveniles showed aggression toward other females and juveniles in similar circumstances and occasionally inflicted superficial wounds. Severe aggression by males, which involved body contact and sometimes biting, was less common and also more puzzling, since there was no apparent cause.

An explanation for at least some of these attacks emerged one day when I was watching Pegasus, a young adult male,

and his friend Cicily, sitting together in the middle of a small clearing. Cicily moved to the edge of the clearing to feed, and a higher-ranking female, Zora, suddenly attacked her. Pegasus stood up and looked as if he were about to intervene when both females disappeared into the bushes. He sat back down, and I remained with him. A full ten minutes later, Zora appeared at the edge of the clearing; this was the first time she had come into view since her attack on Cicily. Pegasus instantly pounced on Zora, repeatedly grabbed her neck in his mouth and lifted her off the ground, shook her whole body, and then dropped her. Zora screamed continuously and tried to escape. Each time, Pegasus caught her and continued his brutal attack. When he finally released her five minutes later she had a deep canine gash on the palm of her hand that made her limp for several days.

This attack was similar in form and intensity to those I had seen before and labeled "unprovoked." Certainly, had I come upon the scene after Zora's aggression toward Cicily, I would not have understood why Pegasus attacked Zora. This suggested that some, perhaps many, severe attacks by males actually represented punishment for actions that had occurred some time before.

Whatever the reasons for male attacks on females, they represent a serious threat. Records of fresh injuries indicated that Eburru Cliffs adult females received canine slash wounds from males at the rate of one for every female each year, and during my study, one female died of her injuries. Males probably pose an even greater threat to infants. Although only one infant was killed during my study, observers in Botswana and Tanzania have seen recent male immigrants kill several young infants.

Protection from male aggression, and from the less injurious but more frequent aggression of other females and juveniles, seems to be one of the main advantages of friendship for a female baboon. Seventy times I observed an adult male defend a female or her offspring against aggression by another troop member, not infrequently a high-ranking male. In all but six of these cases, the defender was a friend. Very few of these confrontations involved actual fighting; no male baboon, subordinate or dominant, is anxious to risk injury by the sharp canines of another.

Males are particularly solicitous guardians of their friends' youngest infants. If another male gets too close to an infant or if a juvenile female plays with it too roughly, the friend may intervene. Other troop members soon learn to be cautious when the mother's friend is nearby, and his presence provides the mother with a welcome respite from the annoying pokes and prods of curious females and juveniles obsessed with the new baby. Male baboons at Gombe Park in Tanzania and Amboseli Park in Kenya have also been seen rescuing infants from chimpanzees and lions. These several forms of male protection help to explain why females in Eburru Cliffs stuck closer to their friends in the first few months after giving birth than at any other time.

The male-infant relationship develops out of the male's friendship with the mother, but as the infant matures, this new bond takes on a life of its own. My co-worker Nancy Nicolson found that by about nine months of age, infants actively sought out their male friends when the mother was a few yards away,

suggesting that the male may function as an alternative caregiver. This seemed to be especially true for infants undergoing unusually early or severe weaning. (Weaning is generally a gradual, prolonged process, but there is tremendous variation among mothers in the timing and intensity of weaning. See "Mother Baboons," *Natural History*, September 1980). After being rejected by the mother, the crying infant often approached the male friend and sat huddled against him until its whimpers subsided. Two of the infants in Eburru Cliffs lost their mothers when they were still quite young. In each case, their bond with the mother's friend subsequently intensified, and—perhaps as a result—both infants survived.

A close bond with a male may also improve the infant's nutrition. Larger than all other troop members, adult males monopolize the best feeding sites. In general, the personal space surrounding a feeding male is inviolate, but he usually tolerates intrusions by the infants of his female friends, giving them access to choice feeding spots.

Although infants follow their male friends around rather than the reverse, the males seem genuinely attached to their tiny companions. During feeding, the male and infant express their pleasure in each other's company by sharing spirited, antiphonal grunting duets. If the infant whimpers in distress, the male friend is likely to cease feeding, look at the infant, and grunt softly, as if in sympathy, until the whimpers cease. When the male rests, the infants of his female friends may huddle behind him, one after the other, forming a "train," or, if feeling energetic, they may use his body as a trampoline.

When I returned to Eburru Cliffs four years after my initial study ended, several of the bonds formed between males and the infants of their female friends were still intact (in other cases, either the male or the infant or both had disappeared). When these bonds involved recently matured females, their long-time male associates showed no sexual interest in them, even though the females mated with other adult males. Mothers and sons, and usually maternal siblings, show similar sexual inhibitions in baboons and many other primate species.

The development of an intimate relationship between a male and the infant of his female friend raises an obvious question: Is the male the infant's father? To answer this question definitely we would need to conduct genetic analysis, which was not possible for these baboons. Instead, I estimated paternity probabilities from observations of the temporary (a few hours or days) exclusive mating relationships, or consortships, that estrous females form with a series of different males. These estimates were apt to be fairly accurate, since changes in the female's sexual swelling allow one to pinpoint the timing of conception to within a few days. Most females consorted with only two or three males during this period, and these males were termed likely fathers.

In about half the friendships, the male was indeed likely to be the father of his friend's most recent infant, but in the other half he was not—in fact, he had never been seen mating with the female. Interestingly, males who were friends with the mother but not likely fathers nearly always developed a relationship with her infant, while males who had mated with the female but were not her friend usually did not. Thus friendship with

the mother, rather than paternity, seems to mediate the development of male-infant bonds. Recently, a similar pattern was documented for South American capuchin monkeys in a laboratory study in which paternity was determined genetically.

These results fly in the face of a prominent theory that claims males will invest in infants only when they are closely related. If males are not fostering the survival of their own genes by caring for the infant, then why do they do so? I suspected that the key was female choice. If females preferred to mate with males who had already demonstrated friendly behavior, then friendships with mothers and their infants might pay off in the future when the mothers were ready to mate again.

To find out if this was the case, I examined each male's sexual behavior with females he had befriended before they resumed estrus. In most cases, males consorted considerably more often with their friends than with other females. Baboon females typically mate with several different males, including both friends and nonfriends, but prior friendship increased a male's probability of mating with a female above what it would have been otherwise.

This increased probability seemed to reflect female preferences. Females occasionally overtly advertised their disdain for certain males and their desire for others. Zizi's behavior, described above, is a good example. Virgil was not one of her friends, but Cyclops was. Usually, however, females expressed preferences and aversions more subtly. For example, Delphi, a petite adolescent female, found herself pursued by Hector, a middle-aged adult male. She did not run away or refuse to mate with him, but whenever he wasn't watching, she looked around for her friend Homer, an adolescent male. When she succeeded in catching Homer's eye, she narrowed her eyes and flattened her ears against her skull, the friendliest face one baboon can send another. This told Homer she would rather be with him. Females expressed satisfaction with a current consort partner by staying close to him, initiating copulations, and not making advances toward other males. Baboons are very sensitive to such cues, as indicated by an experimental study in which rival hamadryas baboons rarely challenged a male-female pair if the female strongly preferred her current partner. Similarly, in Eburru Cliffs, males were less apt to challenge consorts involving a pair that shared a long-term friendship.

Even though females usually consorted with their friends, they also mated with other males, so it is not surprising that friendships were most vulnerable during periods of sexual activity. In a few cases, the female consorted with another male more often than with her friend, but the friendship survived nevertheless. One female, however, formed a strong sexual bond with a new male. This bond persisted after conception, replacing her previous friendship. My observations suggest that adolescent and young adult females tend to have shorter, less stable friendships than do older females. Some friendships, however, last a very long time. When I returned to Eburru Cliffs six years after my study began, five couples were still together. It is possible that friendships occasionally last for life (baboons probably live twenty to thirty years in the wild), but it will require longer studies, and some very patient scientists to find out.

By increasing both the male's chances of mating in the future and the likelihood that a female's infant will survive, friendship contributes to the reproductive success of both partners. This clarifies the evolutionary basis of friendship-forming tendencies in baboons, but what does friendship mean to a baboon? To answer this question we need to view baboons as sentient beings with feelings and goals not unlike our own in similar circumstances. Consider, for example, the friendship between Thalia and Alexander.

The affair began one evening as Alex and Thalia sat about fifteen feet apart on the sleeping cliffs. It was like watching two novices in a singles bar. Alex stared at Thalia until she turned and almost caught him looking at her. He glanced away immediately, and then she stared at him until his head began to turn toward her. She suddenly became engrossed in grooming her toes. But as soon as Alex looked away, her gaze returned to him. They went on like this for more than fifteen minutes, always with split-second timing. Finally, Alex managed to catch Thalia looking at him. He made the friendly eyes-narrowed, ears-back face and smacked his lips together rhythmically. Thalia froze, and for a second she looked into his eyes. Alex approached, and Thalia, still nervous, groomed him. Soon she calmed down, and I found them still together on the cliffs the next morning. Looking back on this event months later, I realized that it marked the beginning of their friendship. Six years later, when I returned to Eburru Cliffs, they were still friends.

If flirtation forms an integral part of baboon friendship, so does jealousy. Overt displays of jealousy, such as chasing a friend away from a potential rival, occur occasionally, but like humans, baboons often express their emotions in more subtle ways. One evening a colleague and I climbed the cliffs and settled down near Sherlock, who was friends with Cybelle, a middle-aged female still foraging on the ground below the cliffs. I observed Cybelle while my colleague watched Sherlock, and we kept up a running commentary. As long as Cybelle was feeding or interacting with females, Sherlock was relaxed, but each time she approached another male, his body would stiffen, and he would stare intently at the scene below. When Cybelle presented politely to a male who had recently tried to befriend her, Sherlock even made threatening sounds under his breath. Cybelle was not in estrus at the time, indicating that male baboon jealousy extends beyond the sexual arena to include affiliative interactions between a female friend and other males.

Because baboon friendships are embedded in a network of friendly and antagonistic relationships, they inevitably lead to repercussions extending beyond the pair. For example, Virgil once provoked his weaker rival Cyclops into a fight by first attacking Cyclops's friend Phoebe. On another occasion, Sherlock chased Circe, Hector's best friend, just after Hector had chased Antigone, Sherlock's friend.

In another incident, the prime adult male Triton challenged Cyclops's possession of meat. Cyclops grew increasingly tense and seemed about to abandon the prey to the younger male. Then Cyclops's friend Phoebe appeared with her infant Phyllis. Phyllis wandered over to Cyclops. He immediately grabbed her, held her close, and threatened Triton away from the prey.

Because any challenge to Cyclops now involved a threat to Phyllis as well, Triton risked being mobbed by Phoebe and her relatives and friends. For this reason, he backed down. Males frequently use the infants of their female friends as buffers in this way. Thus, friendship involves costs as well as benefits because it makes the participants vulnerable to social manipulation or redirected aggression by others.

Finally, as with humans, friendship seems to mean something different to each baboon. Several females in Eburru Cliffs had only one friend. They were devoted companions. Louise and Pandora, for example, groomed their friend Virgil and no other male. Then there was Leda, who, with five friends, spread herself more thinly than any other female. These contrasting patterns of friendship were associated with striking personality differences. Louise and Pandora were unobtrusive females who hung around quietly with Virgil and their close relatives. Leda seemed to be everywhere at once, playing with infants, fighting with juveniles, and making friends with males. Similar differences were apparent among the males. Some devoted a great deal of time and energy to cultivating friendships with females, while others focused more on challenging other males. Although we probably will never fully understand the basis of these individual differences, they contribute immeasurably to the richness and complexity of baboon society.

Male-female friendships may be widespread among primates. They have been reported for many other groups of savanna baboons, and they also occur in rhesus and Japanese Macaques, capuchin monkeys, and perhaps in bonobos (pygmy chimpanzees). These relationships should give us pause when considering popular scenarios for the evolution of male-female relationships in humans. Most of these scenarios assume that, except for mating, males and females had little to do with one another until the development of a sexual division of labor, when, the story goes, females began to rely on males to provide meat in exchange for gathered food. This, it has been argued,

set up new selection pressures favoring the development of long-term bonds between individual males and females, female sexual fidelity, and as paternity certainty increased, greater male investment in the offspring of these unions. In other words, once women began to gather and men to hunt, presto—we had the nuclear family.

This scenario may have more to do with cultural biases about women's economic dependence on men and idealized views of the nuclear family than with the actual behavior of our hominid ancestors. The nonhuman primate evidence challenges this story in at least three ways.

First, long-term bonds between the sexes can evolve in the absence of a sexual division of labor or food sharing. In our primate relatives, such relationships rest on exchanges of social, not economic, benefits.

Second, primate research shows that highly differentiated, emotionally intense male-female relationships can occur without sexual exclusivity. Ancestral men and women may have experienced intimate friendships long before they invented marriage and norms of sexual fidelity.

Third, among our closest primate relatives, males clearly provide mothers and infants with social benefits even when they are unlikely to be the fathers of those infants. In return, females provide a variety of benefits to the friendly males, including acceptance into the group and, at least in baboons, increased mating opportunities in the future. This suggests that efforts to reconstruct the evolution of hominid societies may have overemphasized what the female must supposedly do (restrict her mating to just one male) in order to obtain male parental investment.

Maybe it is time to pay more attention to what the male must do (provide benefits to females and young) in order to obtain female cooperation. Perhaps among our ancestors, as in baboons today, sex and friendship went hand in hand. As for marriage—well, that's another story.

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What's Love Got to Do with It?

Sex among Our Closest Relatives Is a Rather Open Affair

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Maiko and Lana are having sex. Maiko is on top, and Lana's arms and legs are wrapped tightly around his waist. Lina, a friend of Lana's, approaches from the right and taps Maiko on the back, nudging him to finish. As he moves away, Lina enfolds Lana in her arms, and they roll over so that Lana is now on top. The two females rub their genitals together, grinning and screaming in pleasure.

This is no orgy staged for an X-rated movie. It doesn't even involve people—or rather, it involves them only as observers. Lana, Maiko, and Lina are bonobos, a rare species of chimplike ape in which frequent couplings and casual sex play characterize every social relationship—between males and females, members of the same sex, closely related animals, and total strangers. Primatologists are beginning to study the bonobos' unrestrained sexual behavior for tantalizing clues to the origins of our own sexuality.

In reconstructing how early man and woman behaved, researchers have generally looked not to bonobos but to common chimpanzees. Only about 5 million years ago human beings and chimps shared a common ancestor, and we still have much behavior in common: namely, a long period of infant dependency, a reliance on learning what to eat and how to obtain food, social bonds that persist over generations, and the need to deal as a group with many everyday conflicts. The assumption has been that chimp behavior today may be similar to the behavior of human ancestors.

Bonobo behavior, however, offers another window on the past because they, too, shared our 5-million-year-old ancestor, diverging from chimps just 2 million years ago. Bonobos have been less studied than chimps for the simple reason that they are difficult to find. They live only on a small patch of land in Zaire, in central Africa. They were first identified, on the basis of skeletal material, in the 1920s, but it wasn't until the 1970s that their behavior in the wild was studied, and then only sporadically.

Bonobos, also known as pygmy chimpanzees, are not really pygmies but welterweights. The largest males are as big as chimps, and the females of the two species are the same size. But bonobos are more delicate in build, and their arms and legs are long and slender.

On the ground, moving from fruit tree to fruit tree, bonobos often stand and walk on two legs—behavior that makes them seem more like humans than chimps. In some ways their sexual behavior seems more human as well, suggesting that in the sexual arena, at least, bonobos are the more appropriate ancestral model. Males and females frequently copulate face-to-face, which is an uncommon position in animals other than humans. Males usually mount females from behind, but females seem to prefer sex face-to-face. "Sometimes the female will let a male start to mount from behind," says Amy Parish, a graduate student at the University of California at Davis who's been watching female bonobo sexual behavior in several zoo colonies around the world. "And then she'll stop, and of course he's really excited, and then she continues face-to-face." Primatologists assume the female preference is dictated by her anatomy: her enlarged clitoris and sexual swellings are oriented far forward. Females presumably prefer face-to-face contact because it feels better.

"Sex is fun. Sex makes them feel good and keeps the group together."

Like humans but unlike chimps and most other animals, bonobos separate sex from reproduction. They seem to treat sex as a pleasurable activity, and they rely on it as a sort of social glue, to make or break all sorts of relationships. "Ancestral humans behaved like this," proposes Frans de Waal, an ethologist at the Yerkes Regional Primate Research Center at Emory University. "Later, when we developed the family system, the use of sex for this sort of purpose became more limited, mainly occurring within families. A lot of the things we see, like pedophilia and homosexuality, may be leftovers that some now consider unacceptable in our particular society."

Depending on your morals, watching bonobo sex play may be like watching humans at their most extreme and perverse. Bonobos seem to have sex more often and in more combinations than the average person in any culture, and most of the time bonobo sex has nothing to do with making babies. Males mount

females and females sometimes mount them back; females rub against other females just for fun; males stand rump to rump and press their scrotal areas together. Even juveniles participate by rubbing their genital areas against adults, although ethologists don't think that males actually insert their penises into juvenile females. Very young animals also have sex with each other: little males suck on each other's penises or French-kiss. When two animals initiate sex, others freely join in by poking their fingers and toes into the moving parts.

One thing sex does for bonobos is decrease tensions caused by potential competition, often competition for food. Japanese primatologists observing bonobos in Zaire were the first to notice that when bonobos come across a large fruiting tree or encounter piles of provisioned sugarcane, the sight of food triggers a binge of sex. The atmosphere of this sexual free-for-all is decidedly friendly, and it eventually calms the group down. "What's striking is how rapidly the sex drops off," says Nancy Thompson-Handler of the State University of New York at Stony Brook, who has observed bonobos at a site in Zaire called Lomako. "After ten minutes, sexual behavior decreases by fifty percent." Soon the group turns from sex to feeding.

But it's tension rather than food that causes the sexual excitement. "I'm sure the more food you give them, the more sex you'll get," says De Waal. "But it's not really the food, it's competition that triggers this. You can throw in a cardboard box and you'll get sexual behavior." Sex is just the way bonobos deal with competition over limited resources and with the normal tensions caused by living in a group. Anthropologist Frances White of Duke University, a bonobo observer at Lomako since 1983, puts it simply: "Sex is fun. Sex makes them feel good and therefore keeps the group together."

"Females rule the business. It's a good species for feminists, I think."

Sexual behavior also occurs after aggressive encounters, especially among males. After two males fight, one may reconcile with his opponent by presenting his rump and backing up against the other's testicles. He might grab the penis of the other male and stroke it. It's the male bonobo's way of shaking hands and letting everyone know that the conflict has ended amicably.

Researchers also note that female bonobo sexuality, like the sexuality of female humans, isn't locked into a monthly cycle. In most other animals, including chimps, the female's interest in sex is tied to her ovulation cycle. Chimp females sport pink swellings on their hind ends for about two weeks, signaling their fertility, and they're only approachable for sex during that time. That's not the case with humans, who show no outward signs that they are ovulating, and can mate at all phases of the cycle. Female bonobos take the reverse tack, but with similar results. Their large swellings are visible for weeks before and after their fertile periods, and there is never any discernibly wrong time to mate. Like humans, they have sex whether or not they are ovulating.

What's fascinating is that female bonobos use this boundless sexuality in all their relationships. "Females rule the business—sex and food," says De Waal. "It's a good species for feminists, I think." For instance, females regularly use sex to cement relationships with other females. A genital-genital rub, better known as GG-rubbing by observers, is the most frequent behavior used by bonobo females to reinforce social ties or relieve tension. GG-rubbing takes a variety of forms. Often one female rolls on her back and extends her arms and legs. The other female mounts her and they rub their swellings right and left for several seconds, massaging their clitorises against each other. GG-rubbing occurs in the presence of food because food causes tension and excitement, but the intimate contact has the effect of making close friends.

Sometimes females would rather GG-rub with each other than copulate with a male. Parish filmed a 15-minute scene at a bonobo colony at the San Diego Wild Animal Park in which a male, Vernon, repeatedly solicited two females, Lisa and Loretta. Again and again he arched his back and displayed his erect penis—the bonobo request for sex. The females moved away from him, tactfully turning him down until they crept behind a tree and GG-rubbed with each other.

Unlike most primate species, in which males usually take on the dangerous task of leaving home, among bonobos females are the ones who leave the group when they reach sexual maturity, around the age of eight, and work their way into unfamiliar groups. To aid in their assimilation into a new community, the female bonobos make good use of their endless sexual favors. While watching a bonobo group at a feeding tree, White saw a young female systematically have sex with each member before feeding. "An adolescent female, presumably a recent transfer female, came up to the tree, mated with all five males, went into the tree, and solicited GG-rubbing from all the females present," says White.

Once inside the new group, a female bonobo must build a sisterhood from scratch. In groups of humans or chimps, unrelated females construct friendships through the rituals of shopping together or grooming. Bonobos do it sexually. Although pleasure may be the motivation behind a female-female assignation, the function is to form an alliance.

These alliances are serious business, because they determine the pecking order at food sites. Females with powerful friends eat first, and subordinate females may not get any food at all if the resource is small. When times are rough, then, it pays to have close female friends. White describes a scene at Lomako in which an adolescent female, Blanche, benefited from her established friendship with Freda. "I was following Freda and her boyfriend, and they found a tree that they didn't expect to be there. It was a small tree, heavily in fruit with one of their favorites. Freda went straight up the tree and made a food call to Blanche. Blanche came tearing over—she was quite far away—and went tearing up the tree to join Freda, and they GG-rubbed like crazy."

Alliances also give females leverage over larger, stronger males who otherwise would push them around. Females have discovered there is strength in numbers. Unlike other species of primates, such as chimpanzees or baboons (or, all too often,

Hidden Heat

Standing upright is not a position usually—or easily—associated with sex. Among people, at least, anatomy and gravity prove to be forbidding obstacles. Yet our two-legged stance may be the key to a distinctive aspect of human sexuality: the independence of women's sexual desires from a monthly calendar.

Males in the two species most closely related to us, chimpanzees and bonobos, don't spend a lot of time worrying, "Is she interested or not?" The answer is obvious. When ovulatory hormones reach a monthly peak in female chimps and bonobos, and their eggs are primed for fertilization, their genital area swells up, and both sexes appear to have just one thing on their mind. "These animals really turn on when this happens. Everything else is dropped," says primatologist Frederick Szalay of Hunter College in New York.

Women, however, don't go into heat. And this departure from our relatives' sexual behavior has long puzzled researchers. Clear signals of fertility and the willingness to do something about it bring major evolutionary advantages: ripe eggs lead to healthier pregnancies, which leads to more of your genes in succeeding generations, which is what evolution is all about. In addition, male chimps give females that are waving these red flags of fertility first chance at high-protein food such as meat.

So why would our ancestors give this up? Szalay and graduate student Robert Costello have a simple explanation. Women gave heat up, they say, because our ancestors stood up. Fossil footprints indicate that somewhere around 3.5 million years ago hominids—non-ape primates—began walking on two legs. "In hominids, something dictated getting up. We don't know what it was," Szalay says. "But once it did, there was a problem with the signaling system." The problem was that it didn't work. Swollen genital areas that were visible when their owners were down on all fours became hidden between the legs. The mating signal was lost.

"Uprightness meant very tough times for females working with the old ovarian cycle," Szalay says. Males wouldn't notice them, and the swellings themselves, which get quite large, must have made it hard for two-legged creatures to walk around.

Those who found a way out of this quandary, Szalay suggests, were females with small swellings but with a little less hair on their rears and a little extra fat. It would have looked a bit like the time-honored mating signal. They got more attention, and produced more offspring. "You don't start a completely new trend in signaling," Szalay says. "You have a little extra fat, a little nakedness to mimic the ancestors. If there was an ever-so-little advantage because, quite simply, you look good, it would be selected for."

And if a little nakedness and a little fat worked well, Szalay speculates, then a lot of both would work even better. "Once you start a trend in sexual signaling, crazy things happen," he notes. "It's almost like: let's escalate, let's add more. That's what happens in horns with sheep. It's a particular part of the body that brings an advantage." In a few million years human ancestors were more naked than ever, with fleshy rears not found in any other primate. Since these features were permanent, unlike the monthly ups and downs of swellings, sex was free to become a part of daily life.

It's a provocative notion, say Szalay's colleagues, but like any attempt to conjure up the past from the present, there's no real proof of cause and effect. Anthropologist Helen Fisher of the American Museum of Natural History notes that Szalay is merely assuming that fleshy buttocks evolved because they were sex signals. Yet their mass really comes from muscles, which chimps don't have, that are associated with walking. And anthropologist Sarah Blaffer Hrdy of the University of California at Davis points to a more fundamental problem: our ancestors may not have had chimplike swellings that they needed to dispense with. Chimps and bonobos are only two of about 200 primate species, and the vast majority of those species don't have big swellings. Though they are our closest relatives, chimps and bonobos have been evolving during the last 5 million years just as we have, and swollen genitals may be a recent development. The current unswollen human pattern may be the ancestral one.

"Nobody really knows what happened," says Fisher. "Everybody has an idea. You pay your money and you take your choice."

—Joshua Fischman

humans), where tensions run high between males and females, bonobo females are not afraid of males, and the sexes mingle peacefully. "What is consistently different from chimps," says Thompson-Handler, "is the composition of parties. The vast majority are mixed, so there are males and females of all different ages."

Female bonobos cannot be coerced into anything, including sex. Parish recounts an interaction between Lana and a male called Akili at the San Diego Wild Animal Park. "Lana had just been introduced into the group. For a long time she lay on the grass with a huge swelling. Akili would approach her with a big erection and hover over her. It would have been easy for him to do a mount. But he wouldn't. He just kept trying to catch her eye, hovering around her, and she would scoot around the

ground, avoiding him. And then he'd try again. She went around full circle." Akili was big enough to force himself on her. Yet he refrained.

In another encounter, a male bonobo was carrying a large clump of branches. He moved up to a female and presented his erect penis by spreading his legs and arching his back. She rolled onto her back and they copulated. In the midst of their joint ecstasy, she reached out and grabbed a branch from the male. When he pulled back, finished and satisfied, she moved away, clutching the branch to her chest. There was no tension between them, and she essentially traded copulation for food. But the key here is that the male allowed her to move away with the branch—it didn't occur to him to threaten her, because their status was virtually equal.

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Although the results of sexual liberation are clear among bonobos, no one is sure why sex has been elevated to such a high position in this species and why it is restricted merely to reproduction among chimpanzees. "The puzzle for me," says De Waal, "is that chimps do all this bonding with kissing and embracing, with body contact. Why do bonobos do it in a sexual manner?" He speculates that the use of sex as a standard way to underscore relationships began between adult males and adult females as an extension of the mating process and later spread to all members of the group. But no one is sure exactly how this happened.

It is also unclear whether bonobo sexually became exaggerated only after their split from the human lineage or whether the behavior they exhibit today is the modern version of our common ancestor's sex play. Anthropologist Adrienne Zihlman of the University of California at Santa Cruz, who has used the evidence of fossil bones to argue that our earliest known non-ape ancestors, the australopithecines, had body proportions

similar to those of bonobos, says, "The path of evolution is not a straight line from either species, but what I think is important is that the bonobo information gives us more possibilities for looking at human origins."

Some anthropologists, however, are reluctant to include the details of bonobo life, such as wide-ranging sexuality and a strong sisterhood, into scenarios of human evolution. "The researchers have all these commitments to male dominance [as in chimpanzees], and yet bonobos have egalitarian relationships," says De Waal. "They also want to see humans as unique, yet bonobos fit very nicely into many of the scenarios, making humans appear less unique."

Our divergent, non-ape path has led us away from sex and toward a culture that denies the connection between sex and social cohesion. But bonobos, with their versatile sexuality, are here to remind us that our heritage may very well include a primordial urge to make love, not war.

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Apes of Wrath

BARBARA SMUTS

Nearly 20 years ago I spent a morning dashing up and down the hills of Gombe National Park in Tanzania, trying to keep up with an energetic young female chimpanzee, the focus of my observations for the day. On her rear end she sported the small, bright pink swelling characteristic of the early stages of estrus, the period when female mammals are fertile and sexually receptive. For some hours our run through the park was conducted in quiet, but then, suddenly, a chorus of male chimpanzee pant hoots shattered the tranquility of the forest. My female rushed forward to join the males. She greeted each of them, bowing and then turning to present her swelling for inspection. The males examined her perfunctorily and resumed grooming one another, showing no further interest.

Some female primates use social bonds to escape male aggression. Can women?

At first I was surprised by their indifference to a potential mate. Then I realized that it would be many days before the female's swelling blossomed into the large, shiny sphere that signals ovulation. In a week or two, I thought, these same males will be vying intensely for a chance to mate with her.

The attack came without warning. One of the males charged toward us, hair on end, looking twice as large as my small female and enraged. As he rushed by he picked her up, hurled her to the ground, and pummeled her. She cringed and screamed. He ran off, rejoining the other males seconds later as if nothing had happened. It was not so easy for the female to return to normal. She whimpered and darted nervous glances at her attacker, as if worried that he might renew his assault.

In the years that followed I witnessed many similar attacks by males against females, among a variety of Old World primates, and eventually I found this sort of aggression against females so puzzling that I began to study it systematically—something that has rarely been done. My long-term research on olive baboons in Kenya showed that, on average, each pregnant or lactating female was attacked by an adult male about once a week and seriously injured about once a year. Estrous females were the target of even more aggression. The obvious question was, Why?

In the late 1970s, while I was in Africa among the baboons, feminists back in the United States were turning their attention to male violence against women. Their concern stimulated a wave of research documenting disturbingly high levels of battering, rape, sexual harassment, and murder. But although scientists investigated this kind of behavior from many perspectives, they mostly ignored the existence of similar behavior in other animals. My observations over the years have convinced me that a deeper understanding of male aggression against females in other species can help us understand its counterpart in our own.

Researchers have observed various male animals—including insects, birds, and mammals—chasing, threatening, and attacking females. Unfortunately, because scientists have rarely studied such aggression in detail, we do not know exactly how common it is. But the males of many of these species are most aggressive toward potential mates, which suggests that they sometimes use violence to gain sexual access.

Jane Goodall provides us with a compelling example of how males use violence to get sex. In her 1986 book, *The Chimpanzees of Gombe*, Goodall describes the chimpanzee dating game. In one of several scenarios, males gather around attractive estrous females and try to lure them away from other males for a one-on-one sexual expedition that may last for days or weeks. But females find some suitors more appealing than others and often resist the advances of less desirable males. Males often rely on aggression to counter female resistance. For example, Goodall describes how Evered, in "persuading" a reluctant Winkle to accompany him into the forest, attacked her six times over the course of five hours, twice severely.

Sometimes, as I saw in Gombe, a male chimpanzee even attacks an estrous female days before he tries to mate with her. Goodall thinks that a male uses such aggression to train a female to fear him so that she will be more likely to surrender to his subsequent sexual advances. Similarly, male hamadryas baboons, who form small harems by kidnapping child brides, maintain a tight rein over their females through threats and intimidation. If, when another male is nearby, a hamadryas female strays even a few feet from her mate, he shoots her a threatening stare and raises his brows. She usually responds by rushing to his side; if not, he bites the back of her neck. The neck bite is ritualized—the male does not actually sink his

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razor-sharp canines into her flesh—but the threat of injury is clear. By repeating this behavior hundreds of times, the male lays claim to particular females months or even years before mating with them. When a female comes into estrus, she solicits sex only from her harem master, and other males rarely challenge his sexual rights to her.

In some species, females remain in their birth communities their whole lives, joining forces with related females to defend vital food resources against other females.

These chimpanzee and hamadryas males are practicing sexual coercion: male use of force to increase the chances that a female victim will mate with him, or to decrease the chances that she will mate with someone else. But sexual coercion is much more common in some primate species than in others. Orangutans and chimpanzees are the only nonhuman primates whose males in the wild force females to copulate, while males of several other species, such as vervet monkeys and bonobos (pygmy chimpanzees), rarely if ever try to coerce females sexually. Between the two extremes lie many species, like hamadryas baboons, in which males do not force copulation but nonetheless use threats and intimidation to get sex.

These dramatic differences between species provide an opportunity to investigate which factors promote or inhibit sexual coercion. For example, we might expect to find more of it in species in which males are much larger than females—and we do. However, size differences between the sexes are far from the whole story. Chimpanzee and bonobo males both have only a slight size advantage, yet while male chimps frequently resort to force, male bonobos treat the fair sex with more respect. Clearly, then, although size matters, so do other factors. In particular, the social relationships females form with other females and with males appear to be as important.

In some species, females remain in their birth communities their whole lives, joining forces with related females to defend vital food resources against other females. In such “female bonded” species, females also form alliances against aggressive males. Vervet monkeys are one such species, and among these small and exceptionally feisty African monkeys, related females gang up against males. High-ranking females use their dense network of female alliances to rule the troop; although smaller than males, they slap persistent suitors away like annoying flies. Researchers have observed similar alliances in many other female-bonded species, including other Old World monkeys such as macaques, olive baboons, patas and rhesus monkeys, and gray langurs; New World monkeys such as the capuchin; and prosimians such as the ring-tailed lemur.

Females in other species leave their birth communities at adolescence and spend the rest of their lives cut off from their female kin. In most such species, females do not form strong bonds with other females and rarely support one another against males. Both chimpanzees and hamadryas baboons exhibit this

pattern, and, as we saw earlier, in both species females submit to sexual control by males.

Some of the factors that influence female vulnerability to male sexual coercion in different species may also help explain such variation among different groups in the same species.

This contrast between female-bonded species, in which related females gang together to thwart males, and non-female-bonded species, in which they don't, breaks down when we come to the bonobo. Female bonobos, like their close relatives the chimpanzees, leave their kin and live as adults with unrelated females. Recent field studies show that these unrelated females hang out together and engage in frequent homoerotic behavior, in which they embrace face-to-face and rapidly rub their genitals together; sex seems to cement their bonds. Examining these studies in the context of my own research has convinced me that one way females use these bonds is to form alliances against males, and that, as a consequence, male bonobos do not dominate females or attempt to coerce them sexually. How and why female bonobos, but not chimpanzees, came up with this solution to male violence remains a mystery.

Female primates also use relationships with males to help protect themselves against sexual coercion. Among olive baboons, each adult female typically forms long-lasting “friendships” with a few of the many males in her troop. When a male baboon assaults a female, another male often comes to her rescue; in my troop, nine times out of ten the protector was a friend of the female's. In return for his protection, the defender may enjoy her sexual favors the next time she comes into estrus. There is a dark side to this picture, however. Male baboons frequently threaten or attack their female friends—when, for example, one tries to form a friendship with a new male. Other males apparently recognize friendships and rarely intervene. The female, then, becomes less vulnerable to aggression from males in general, but more vulnerable to aggression from her male friends.

As a final example, consider orangutans. Because their food grows so sparsely adult females rarely travel with anyone but their dependent offspring. But orangutan females routinely fall victim to forced copulation. Female orangutans, it seems, pay a high price for their solitude.

Some of the factors that influence female vulnerability to male sexual coercion in different species may also help explain such variation among different groups in the same species. For example, in a group of chimpanzees in the Tai Forest in the Ivory Coast, females form closer bonds with one another than do females at Gombe. Tai females may consequently have more egalitarian relationships with males than their Gombe counterparts do.

Such differences between groups especially characterize humans. Among the South American Yanomamö, for instance, men frequently abduct and rape women from neighboring villages and severely beat their wives for suspected adultery. However, among the Aka people of the Central African Republic, male aggression against women has never been observed. Most human societies, of course, fall between these two extremes.

How are we to account for such variation? The same social factors that help explain how sexual coercion differs among nonhuman primates may deepen our understanding of how it varies across different groups of people. In most traditional human societies, a woman leaves her birth community when she marries and goes to live with her husband and his relatives. Without strong bonds to close female kin, she will probably be in danger of sexual coercion. The presence of close female kin, though, may protect her. For example, in a community in Belize, women live near their female relatives. A man will sometimes beat his wife if he becomes jealous or suspects her of infidelity, but when this happens, onlookers run to tell her female kin. Their arrival on the scene, combined with the presence of other glaring women, usually shames the man enough to stop his aggression.

Even in societies in which women live away from their families, kin may provide protection against abusive husbands, though how much protection varies dramatically from one society to the next. In some societies a woman's kin, including her father and brothers, consistently support her against an abusive husband, while in others they rarely help her. Why?

The key may lie in patterns of male-male relationships. Alliances between males are much more highly developed in humans than in other primates, and men frequently rely on such alliances to compete successfully against other men. They often gain more by supporting their male allies than they do by supporting female kin. In addition, men often use their alliances to defeat rivals and abduct or rape their women, as painfully illustrated by recent events in Bosnia. When women live far from close kin, among men who value their alliances with other men more than their bonds with women, they may be even more vulnerable to sexual coercion than many nonhuman primate females.

Even in societies in which women live away from their families, kin may provide protection against abusive husbands.

Like nonhuman primate females, many women form bonds with unrelated males who may protect them from other males. However, reliance on men exacts a cost—women and other primate females often must submit to control by their protectors.

Such control is more elaborate in humans because allied men agree to honor one another's proprietary rights over women. In most of the world's cultures, marriage involves not only the exclusion of other men from sexual access to a man's wife—which protects the woman against rape by other men—but also entails the husband's right to complete control over his wife's sexual life, including the right to punish her for real or suspected adultery, to have sex with her whenever he wants, and even to restrict her contact with other people, especially men.

In modern industrial society, many men—perhaps most—maintain such traditional notions of marriage. At the same time, many of the traditional sources of support for women, including censure of abusive husbands by the woman's kinfolk or other community members, are eroding as more and more people end up without nearby kin or long-term neighbors. The increased vulnerability of women isolated from their birth communities, however, is not just a by-product of modern living. Historically, in highly patriarchal societies like those found in China and northern India, married women lived in households ruled by their husband's mother and male kin, and their ties with their own kin were virtually severed. In these societies, today as in the past, the husband's female kin often view the wife as a competitor for resources. Not only do they fail to support her against male coercive control, but they sometimes actively encourage it. This scenario illustrates an important point: women do not invariably support other women against men, in part because women may perceive their interests as best served through alliances with men, not with other women. When men have most of the power and control most of the resources, this looks like a realistic assessment.

Decreasing women's vulnerability to sexual coercion, then, may require fundamental changes in social alliances. Women gave voice to this essential truth with the slogan **SISTERHOOD IS POWERFUL**—a reference to the importance of women's ability to cooperate with unrelated women as if they were indeed sisters. However, among humans, the male-dominant social system derives support from political, economic, legal, and ideological institutions that other primates can't even dream of. Freedom from male control—including male sexual coercion—therefore requires women to form alliances with one another (and with like-minded men) on a scale beyond that shown by nonhuman primates and humans in the past. Although knowledge of other primates can provide inspiration for this task, its achievement depends on the uniquely human ability to envision a future different from anything that has gone before.

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Mothers and Others

SARAH BLAFFER HRDY

Mother apes—chimpanzees, gorillas, orangutans, humans—dote on their babies. And why not? They give birth to an infant after a long gestation and, in most cases, suckle it for years. With humans, however, the job of providing for a juvenile goes on and on. Unlike all other ape babies, ours mature slowly and reach independence late. A mother in a foraging society may give birth every four years or so, and her first few children remain dependent long after each new baby arrives; among nomadic foragers, grown-ups may provide food to children for eighteen or more years. To come up with the 10–13 million calories that anthropologists such as Hillard Kaplan calculate are needed to rear a young human to independence, a mother needs help.

So how did our prehuman and early human ancestresses living in the Pleistocene Epoch (from 1.6 million until roughly 10,000 years ago) manage to get those calories? And under what conditions would natural selection allow a female ape to produce babies so large and slow to develop that they are beyond her means to rear on her own?

The old answer was that fathers helped out by hunting. And so they do. But hunting is a risky occupation, and fathers may die or defect or take up with other females. And when they do, what then? New evidence from surviving traditional cultures suggests that mothers in the Pleistocene may have had a significant degree of help—from men who thought they just might have been the fathers, from grandmothers and great-aunts, from older children.

These helpers other than the mother, called allomothers by sociobiologists, do not just protect and provision youngsters. In groups such as the Efe and Aka Pygmies of central Africa, allomothers actually hold children and carry them about. In these tight-knit communities of communal foragers—within which men, women, and children still hunt with nets, much as humans are thought to have done tens of thousands of years ago—siblings, aunts, uncles, fathers, and grandmothers hold newborns on the first day of life. When University of New Mexico anthropologist Paula Ivey asked an Efe woman, “Who cares for babies?” the immediate answer was, “We all do!” By three weeks of age, the babies are in contact with allomothers 40 percent of the time. By eighteen weeks, infants actually spend more time with allomothers than with their gestational mothers. On average, Efe babies have fourteen different caretakers, most of whom are close kin. According to Washington State University anthropologist Barry Hewlett, Aka babies

are within arm’s reach of their fathers for more than half of every day.

Accustomed to celebrating the antiquity and naturalness of mother-centered models of child care, as well as the nuclear family in which the mother nurtures while the father provides, we Westerners tend to regard the practices of the Efe and the Aka as exotic. But to sociobiologists, whose stock in trade is comparisons across species, all this helping has a familiar ring. It’s called cooperative breeding. During the past quarter century, as anthropologists and sociobiologists started to compare notes, one of the spectacular surprises has been how much allo-maternal care goes on, not just within various human societies but among animals generally. Evidently, diverse organisms have converged on cooperative breeding for the best of evolutionary reasons.

A broad look at the most recent evidence has convinced me that cooperative breeding was the strategy that permitted our own ancestors to produce costly, slow-maturing infants at shorter intervals, to take advantage of new kinds of resources in habitats other than the mixed savanna-woodland of tropical Africa, and to spread more widely and swiftly than any primate had before. We already know that animal mothers who delegate some of the costs of infant care to others are thereby freed to produce more or larger young or to breed more frequently. Consider the case of silver-backed jackals. Patricia Moehlman, of the World Conservation Union, has shown that for every extra helper bringing back food, jackal parents rear one extra pup per litter. Cooperative breeding also helps various species expand into habitats in which they would normally not be able to rear any young at all. Florida scrub-jays, for example, breed in an exposed landscape where unrelenting predation from hawks and snakes usually precludes the fledging of young; survival in this habitat is possible only because older siblings help guard and feed the young. Such cooperative arrangements permit animals as different as naked mole rats (the social insects of the mammal world) and wolves to move into new habitats and sometimes to spread over vast areas.

When animal mothers delegate some infant-care costs to others, they can produce more or larger young and raise them in less-than-ideal habitats.

What does it take to become a cooperative breeder? Obviously, this lifestyle is an option only for creatures capable of living in groups. It is facilitated when young but fully mature individuals (such as young Florida scrub-jays) do not or cannot immediately leave their natal group to breed on their own and instead remain among kin in their natal location. As with delayed maturation, delayed dispersal of young means that teenagers, "spinster" aunts, real and honorary uncles will be on hand to help their kin rear young. Flexibility is another criterion for cooperative breeders. Helpers must be ready to shift to breeding mode should the opportunity arise. In marmosets and tamarins—the little South American monkeys that are, besides us, the only full-fledged cooperative breeders among primates—a female has to be ready to be a helper this year and a mother the next. She may have one mate or several. In canids such as wolves or wild dogs, usually only the dominant, or alpha, male and female in a pack reproduce, but younger group members hunt with the mother and return to the den to regurgitate predigested meat into the mouths of her pups. In a fascinating instance of physiological flexibility, a subordinate female may actually undergo hormonal transformations similar to those of a real pregnancy: her belly swells, and she begins to manufacture milk and may help nurse the pups of the alpha pair. Vestiges of cooperative breeding crop up as well in domestic dogs, the distant descendants of wolves. After undergoing a pseudopregnancy, my neighbors' Jack Russell terrier chased away the family's cat and adopted and suckled her kittens. To suckle the young of another species is hardly what Darwinians call an adaptive trait (because it does not contribute to the surrogate's own survival). But in the environment in which the dog family evolved, a female's tendency to respond when infants signaled their need—combined with her capacity for pseudopregnancy—would have increased the survival chances for large litters born to the dominant female.

According to the late W.D. Hamilton, evolutionary logic predicts that an animal with poor prospects of reproducing on his or her own should be predisposed to assist kin with better prospects so that at least some of their shared genes will be perpetuated. Among wolves, for example, both male and female helpers in the pack are likely to be genetically related to the alpha litter and to have good reasons for not trying to reproduce on their own: in a number of cooperatively breeding species (wild dogs, wolves, hyenas, dingoes, dwarf mongooses, marmosets), the helpers do try, but the dominant female is likely to bite their babies to death. The threat of coercion makes postponing ovulation the better part of valor, the least-bad option for females who must wait to breed until their circumstances improve, either through the death of a higher-ranking female or by finding a mate with an unoccupied territory.

One primate strategy is to line up extra fathers. Among common marmosets and several species of tamarins, females mate with several males, all of which help rear her young. As primatologist Charles T. Snowdon points out, in three of the four genera of Callitrichidae (*Callithrix*, *Saguinus*, and *Leontopithecus*), the more adult males the group has available to help, the more young survive. Among many of these species, females ovulate just after giving birth, perhaps encouraging males to stick around until after babies are born. (In cotton-top tamarins, males also undergo hormonal changes that prepare them to care

for infants at the time of birth.) Among cooperative breeders of certain other species, such as wolves and jackals, pups born in the same litter can be sired by different fathers.

Human mothers, by contrast, don't ovulate again right after birth, nor do they produce offspring with more than one genetic father at a time. Ever inventive, though, humans solve the problem of enlisting help from several adult males by other means. In some cultures, mothers rely on a peculiar belief that anthropologists call *partible paternity*—the notion that a fetus is built up by contributions of semen from all the men with whom women have had sex in the ten months or so prior to giving birth. Among the Canela, a matrilineal tribe in Brazil studied for many years by William Crocker of the Smithsonian Institution, publicly sanctioned intercourse between women and men other than their husbands—sometimes many men—takes place during village-wide ceremonies. What might lead to marital disaster elsewhere works among the Canela because the men believe in *partible paternity*. Across a broad swath of South America—from Paraguay up into Brazil, westward to Peru, and northward to Venezuela—mothers rely on this convenient folk wisdom to line up multiple honorary fathers to help them provision both themselves and their children. Over hundreds of generations, this belief has helped children thrive in a part of the world where food sources are unpredictable and where husbands are as likely as not to return from the hunt empty-handed.

The Bari people of Venezuela are among those who believe in shared paternity, and according to anthropologist Stephen Beckerman, Bari children with more than one father do especially well. In Beckerman's study of 822 children, 80 percent of those who had both a "primary" father (the man married to their mother) and a "secondary" father survived to age fifteen, compared with 64 percent survival for those with a primary father alone. Not surprisingly, as soon as a Bari woman suspects she is pregnant, she accepts sexual advances from the more successful fishermen or hunters in her group. Belief that fatherhood can be shared draws more men into the web of possible paternity, which effectively translates into more food and more protection.

But for human mothers, extra mates aren't the only source of effective help. Older children, too, play a significant role in family survival. University of Nebraska anthropologists Patricia Draper and Raymond Hames have just shown that among !Kung hunters and gatherers living in the Kalahari Desert, there is a significant correlation between how many children a parent successfully raises and how many older siblings were on hand to help during that person's own childhood.

One primate strategy is to line up extra "fathers." In some species of marmosets, females mate with several males, all of which help her raise her young.

Older matrilineal kin may be the most valuable helpers of all. University of Utah anthropologists Kristen Hawkes and James O'Connell and their UCLA colleague Nicholas Blurton Jones,

who have demonstrated the important food-gathering role of older women among Hazda hunter-gatherers in Tanzania, delight in explaining that since human life spans may extend for a few decades after menopause, older women become available to care for—and to provide vital food for—children born to younger kin. Hawkes, O'Connell, and Blurton Jones further believe that dating from the earliest days of *Homo erectus*, the survival of weaned children during food shortages may have depended on tubers dug up by older kin.

At various times in human history, people have also relied on a range of customs, as well as on coercion, to line up allomaternal assistance—for example, by using slaves or hiring poor women as wet nurses. But all the helpers in the world are of no use if they're not motivated to protect, carry, or provision babies. For both humans and nonhumans, this motivation arises in three main ways: through the manipulation of information about kinship; through appealing signals coming from the babies themselves; and, at the heart of it all, from the endocrinological and neural processes that induce individuals to respond to infants' signals. Indeed, all primates and many other mammals eventually respond to infants in a nurturing way if exposed long enough to their signals. Trouble is, "long enough" can mean very different things in males and females, with their very different response thresholds.

For decades, animal behaviorists have been aware of the phenomenon known as priming. A mouse or rat encountering a strange pup is likely to respond by either ignoring the pup or eating it. But presented with pup after pup, rodents of either sex eventually become sensitized to the baby and start caring for it. Even a male may gather pups into a nest and lick or huddle over them. Although nurturing is not a routine part of a male's repertoire, when sufficiently primed he behaves as a mother would. Hormonal change is an obvious candidate for explaining this transformation. Consider the case of the cooperatively breeding Florida scrub-jays studied by Stephan Schoech, of the University of Memphis. Prolactin, a protein hormone that initiates the secretion of milk in female mammals, is also present in male mammals and in birds of both sexes. Schoech showed that levels of prolactin go up in a male and female jay as they build their nest and incubate eggs and that these levels reach a peak when they feed their young. Moreover, prolactin levels rise in the jays' nonbreeding helpers and are also at their highest when they assist in feeding nestlings.

As it happens, male, as well as immature and nonbreeding female, primates can respond to infants' signals, although quite different levels of exposure and stimulation are required to get them going. Twenty years ago, when elevated prolactin levels were first reported in common marmoset males (by Alan Dixson, for *Callithrix jacchus*), many scientists refused to believe it. Later, when the finding was confirmed, scientists assumed this effect would be found only in fathers. But based on work by Scott Nunes, Jeffrey Fite, Jeffrey French, Charles Snowdon, Lucille Roberts, and many others—work that deals with a variety of species of marmosets and tamarins—we now know that all sorts of hormonal changes are associated with increased nurturing in males. For example, in the tufted-eared marmosets studied by French and colleagues, testosterone lev-

els in males went down as they engaged in caretaking after the birth of an infant. Testosterone levels tended to be lowest in those with the most paternal experience.

Genetic relatedness alone, in fact, is a surprisingly unreliable predictor of love. What matters are cues from infants and how we process these cues emotionally.

The biggest surprise, however, has been that something similar goes on in males of our own species. Anne Storey and colleagues in Canada have reported that prolactin levels in men who were living with pregnant women went up toward the end of the pregnancy. But the most significant finding was a 30 percent drop in testosterone in men right after the birth. (Some endocrinologically literate wags have proposed that this drop in testosterone levels is due to sleep deprivation, but this would probably not explain the parallel testosterone drop in marmoset males housed with parturient females.) Hormonal changes during pregnancy and lactation are, of course, indisputably more pronounced in mothers than in the men consorting with them, and no one is suggesting that male consorts are equivalent to mothers. But both sexes are surprisingly susceptible to infant signals—explaining why fathers, adoptive parents, wet nurses, and day-care workers can become deeply involved with the infants they care for.

Genetic relatedness alone, in fact, is a surprisingly unreliable predictor of love. What matters are cues from infants and how these cues are processed emotionally. The capacity for becoming emotionally hooked—or primed—also explains how a fully engaged father who is in frequent contact with his infant can become more committed to the infant's well-being than a detached mother will.

But we can't forget the real protagonist of this story: the baby. From birth, newborns are powerfully motivated to stay close, to root—even to creep—in quest of nipples, which they instinctively suck on. These are the first innate behaviors that any of us engage in. But maintaining contact is harder for little humans to do than it is for other primates. One problem is that human mothers are not very hairy, so a human mother not only has to position the baby on her breast but also has to keep him there. She must be motivated to pick up her baby even *before* her milk comes in, bringing with it a host of hormonal transformations.

Within minutes of birth, human babies can cry and vocalize just as other primates do, but human newborns can also read facial expressions and make a few of their own. Even with blurry vision, they engage in eye-to-eye contact with the people around them. Newborn babies, when alert, can see about eighteen inches away. When people put their faces within range, babies may reward this attention by looking back or even imitating facial expressions. Orang and chimp babies, too, are strongly attached to and interested in their mothers' faces. But unlike humans, other ape mothers and infants do not get absorbed in gazing deeply into each other's eyes.

What conclusion can we draw from all this? Instead of arguing over "mother care" versus "other care," we need to make day care better. And this is where I think today's evolution-minded researchers have something to say. Impressed by just how variable child-rearing conditions can be in human societies, several anthropologists and psychologists (including Michael Lamb, Patricia Draper, Henry Harpending, and James Chisholm) have suggested that babies are up to more than just maintaining the relationship with their mothers. These researchers propose that babies actually monitor mothers to gain information about the world they have been born into. Babies ask, in effect, Is this world filled with people who are going to provide for me and help me survive? Can I count on them to care about me? If the answer to those questions is yes, they begin to sense that developing a conscience and a capacity for compassion would be a great idea. If the answer is no, they may then be asking, Can I not afford to count on others? Would I be better off just grabbing what I need, however I can? In this case, empathy, or thinking about others' needs, would be more of a hindrance than a help.

For a developing baby and child, the most practical way to behave might vary drastically, depending on whether the mother has kin who help, whether the father is around, whether foster parents are well-meaning or exploitative. These factors, however unconsciously perceived by the child, affect important developmental decisions. Being extremely self-centered or selfish, being oblivious to others or lacking in conscience—traits that psychologists and child-development theorists may view as pathological—are probably quite adaptive traits for an individual who is short on support from other group members.

If I am right that humans evolved as cooperative breeders, Pleistocene babies whose mothers lacked social support and were less than fully committed to infant care would have been unlikely to survive. But once people started to settle down—10,000 or 20,000 or perhaps 30,000 years ago—the picture changed. Ironically, survival chances for neglected children increased. As people lingered longer in one place, eliminated predators, built walled houses, stored food—not to mention inventing things such as rubber nipples and pasteurized milk—infant survival became decoupled from continuous contact with a caregiver.

Since the end of the Pleistocene, whether in preindustrial or industrialized environments, some children have been surviving levels of social neglect that previously would have meant certain death. Some children get very little attention, even in the most benign of contemporary homes. In the industrialized world, children routinely survive caretaking practices that an Efe or a !Kung mother would find appallingly negligent. In traditional societies, no decent mother leaves her baby alone at any time, and traditional mothers are shocked to learn that Western mothers leave infants unattended in a crib all night.

In effect, babies ask: Is this world filled with people who are going to provide for me and help me survive? Can I count on them to care about me?

Without passing judgment, one may point out that only in the recent history of humankind could infants deprived of supportive human contact survive to reproduce themselves. Certainly there are a lot of humanitarian reasons to worry about this situation: one wants each baby, each child, to be lovingly cared for. From my evolutionary perspective, though, even more is at stake.

Even if we manage to survive what most people are worrying about—global warming, emergent diseases, rogue viruses, meteorites crashing into earth—will we still be human thousands of years down the line? By that I mean human in the way we currently define ourselves. The reason our species has managed to survive and proliferate to the extent that 6 billion people currently occupy the planet has to do with how readily we can learn to cooperate when we want to. And our capacity for empathy is one of the things that made us good at doing that.

At a rudimentary level, of course, all sorts of creatures are good at reading intentions and movements and anticipating what other animals are going to do. Predators from gopher snakes to lions have to be able to anticipate where their quarry will dart. Chimps and gorillas can figure out what another individual is likely to know or not know. But compared with that of humans, this capacity to entertain the psychological perspective of other individuals is crude.

During early childhood, through relationships with mothers and other caretakers, individuals learn to look at the world from someone else's perspective.

The capacity for empathy is uniquely well developed in our species, so much so that many people (including me) believe that along with language and symbolic thought, it is what makes us human. We are capable of compassion, of understanding other people's "fears and motives, their longings and griefs and vanities," as novelist Edmund White puts it. We spend time and energy worrying about people we have never even met, about babies left in dumpsters, about the existence of more than 12 million AIDS orphans in Africa.

Psychologists know that there is a heritable component to emotional capacity and that this affects the development of compassion among individuals. By fourteen months of age, identical twins (who share all genes) are more alike in how they react to an experimenter who pretends to painfully pinch her finger on a clipboard than are fraternal twins (who share only half their genes). But empathy also has a learned component, which has more to do with analytical skills. During the first years of life, within the context of early relationships with mothers and other committed caretakers, each individual learns to look at the world from someone else's perspective.

And this is why I get so worried. Just because humans have evolved to be smart enough to chronicle our species' histories, to speculate about its origins, and to figure out that we have

happens to be a good indicator of her social supports. In terms of developmental outcomes, the most relevant factor might not be how securely or insecurely attached to the mother the baby is—the variable that developmental psychologists are trained to measure—but rather how secure the baby is in relation to all the people caring for him or her. Measuring attachment this way might help explain why even children whose relations with their mother suggest they are at extreme risk manage to do fine because of the interventions of a committed father, an older sibling, or a there-when-you-need-her grandmother.

The most comprehensive study ever done on how nonmaternal care affects kids is compatible with both the hypothesis that humans evolved as cooperative breeders and the conventional hypothesis that human babies are adapted to be reared exclusively by mothers. Undertaken by the National Institute of Child Health and Human Development (NICHD) in 1991, the seven-year study included 1,364 children and their families (from diverse ethnic and economic backgrounds) and was conducted in ten different U.S. locations. This extraordinarily ambitious study was launched because statistics showed that 62 percent of U.S. mothers with children under age six were working outside the home and that the majority of them (willingly or unwillingly) were back at work within three to five months of giving birth. Because this was an entirely new social phenomenon, no one really knew what the NICHD's research would reveal.

The study's main finding was that both maternal and hired caretakers' sensitivity to infant needs was a better predictor of a child's subsequent development and behavior (such traits as social "competence," respect for others, and self-control were measured) than was actual time spent apart from the mother. In other words, the critical variable was not the continuous presence of the mother herself but rather how secure infants felt when cared for by someone else. People who had been convinced that babies need full-time care from mothers to develop normally were stunned by these results, while advocates of day care felt vindicated. But do these and other, similar findings mean that day care is not something we need to worry about anymore?

Not at all. We should keep worrying. The NICHD study showed only that day care was better than mother care if the mother was neglectful or abusive. But excluding such worst-case scenarios, the study showed no detectable ill effects from day care only when infants had a secure relationship with parents to begin with (which I take to mean that babies felt wanted) and only when the day care was of high quality. And in this study's context, "high quality" meant that the facility had a high ratio of caretakers to babies, that it had the same caretakers all the time, and that the caretakers were sensitive to infants' needs—in other words, that the day care staff acted like committed kin.

Bluntly put, this kind of day care is almost impossible to find. Where it exists at all, it's expensive. Waiting lists are long, even for cheap or inadequate care. The average rate of staff turnover in day care centers is 30 percent per year, primarily because these workers are paid barely the minimum wage (usually less, in fact, than parking-lot attendants). Furthermore, day care tends to be age-graded, so even at centers where staff members stay put, kids move annually to new teachers. This kind of day care is unlikely to foster trusting relationships.

To the extent that psychiatrists and pediatricians have thought about this difference between us and the other apes, they tend to attribute it to human mental agility and our ability to use language. Interactions between mother and baby, including vocal play and babbling, have been interpreted as protoconversations: revving up the baby to learn to talk. Yet even babies who lack face-to-face stimulation—babies born blind, say—learn to talk. Furthermore, humans are not the only primates to engage in the continuous rhythmic streams of vocalization known as babbling. Interestingly, marmoset and tamarin babies also babble. It may be that the infants of cooperative breeders are specially equipped to communicate with caretakers. This is not to say that babbling is not an important part of learning to talk, only to question which came first—babbling so as to develop into a talker, or a predisposition to evolve into a talker because among cooperative breeders, babies that babble are better tended and more likely to survive.

If humans evolved as cooperative breeders, the degree of a human mother's commitment to her infant should be linked to how much social support she herself can expect. Mothers in cooperatively breeding primate species can afford to bear and rear such costly offspring as they do only if they have help on hand. Maternal abandonment and abuse are very rarely observed among primates in the wild. In fact, the only primate species in which mothers are anywhere near as likely to abandon infants at birth as mothers in our own species are the other cooperative breeders. A study of cotton-top tamarins at the New England Regional Primate Research Center showed a 12 percent chance of abandonment if mothers had older siblings on hand to help them rear twins, but a 57 percent chance when no help was available. Overburdened mothers abandoned infants within seventy-two hours of birth.

This new way of thinking about our species' history, with its implications for children, has made me concerned about the future. So far, most Western researchers studying infant development have presumed that living in a nuclear family with a fixed division of labor (mom nurturing, dad providing) is the normal human adaptation. Most contemporary research on children's psychosocial development is derived from John Bowlby's theories of attachment and has focused on such variables as how available and responsive the mother is, whether the father is present or absent, and whether the child is in the mother's care or in day care. Sure enough, studies done with this model in mind always show that children with less responsive mothers are at greater risk.

In cooperative breeders, the degree of a mother's commitment to her infant should correlate with how much social support she herself can expect.

It is the baby, first and foremost, who senses how available and how committed its mother is. But I know of no studies that take into account the possibility that humans evolved as cooperative breeders and that a mother's responsiveness also

about 30,000 genes in our genome is no reason to assume that evolution has come to a standstill. As gene frequencies change, natural selection acts on the outcome, the expression of those genes. No one doubts, for instance, that fish benefit from being able to see. Yet species reared in total darkness—as are the small, cave-dwelling characin of Mexico—fail to develop their visual capacity. Through evolutionary time, traits that are unexpressed are eventually lost. If populations of these fish are isolated in caves long enough, youngsters descended from those original populations will no longer be able to develop eyesight at all, even if reared in sunlight.

If human compassion develops only under particular rearing conditions, and if an increasing proportion of the species survives to breeding age without developing compassion, it won't

make any difference how useful this trait was among our ancestors. It will become like sight in cave-dwelling fish.

No doubt our descendants thousands of years from now (should our species survive) will still be bipedal, symbol-generating apes. Most likely they will be adept at using sophisticated technologies. But will they still be human in the way we, shaped by a long heritage of cooperative breeding, currently define ourselves?

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