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The Social Behavior of Chimpanzees and Bonobos

Empirical Evidence and Shifting Assumptions[1]

by Craig B. Stanford

As our closest living relatives, chimpanzees and bonobos have been widely used as models of the behavior of early hominids. In recent years, as information on the social behavior and ecology of bonobos has come to light, many interspecific comparisons have been made. Chimpanzees have been characterized in terms of their intercommunity warfare, meat eating, infanticide, cannibalism, male status-striving, and dominance over females. Bonobos, meanwhile, have been portrayed as the "Make love, not war" ape, characterized by female power-sharing, a lack of aggression between either individuals or groups, richly elaborated sexual behavior that occurs without the constraint of a narrow window of fertility, and the use of sex for communicative purposes. This paper evaluates the evidence for this dichotomy and considers the reasons that contrasting portrayals of the two great apes have developed. While there are marked differences in social behavior between these two species, I argue that they are more similar behaviorally than most accounts have suggested. I discuss several reasons that current views of bonobo and chimpanzee societies may not accord well with field data. Among these are a bias toward captive data on bonobos, the tendency to see bonobos as derived because their behavior has been described more recently than that of chimpanzees, and the possibility that interpretations of bonobo-chimpanzee differences are reflections of human male-female differences.

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Molecular studies indicate that humans, chimpanzees (*Pan troglodytes*), and bonobos (*P. paniscus*) are very closely related in a lineage that split into hominid and *Pan* lines approximately 6–7 million years ago, possibly following a divergence from the gorilla lineage about 1–2 million years earlier (Caccone and Powell 1989, Ruvolo et al. 1991). Chimpanzees and bonobos have a more recent common ancestry only some 2–2.5 million years ago (Caccone and Powell 1989). Although it is now an endangered species, the chimpanzee is an extremely successful species ecologically, occurring in a wide range of habitat types across the equatorial portion of the African continent. The bonobo, by contrast, is found in a much more geographically and ecologically restricted region of lowland rain forest in central Zaïre. Until the 1980s, so little was known about the behavior of wild bonobos that detailed comparisons between the two *Pan* species were not possible. The number of field observation hours on bonobos is today still a small fraction of the database of chimpanzee behavior and ecology (White 1996*a*), but cross-species comparisons are nevertheless commonplace.

These two African apes have been reported to differ dramatically in patterns of sexuality, dominance, same-sex social bonds, and the frequency and intensity of both intragroup and intergroup aggression. Chimpanzees have long been described in terms of male dominance over females, hunting and meat eating, and intercommunity warfare. According to Wrangham and Peterson (1996:191), "What most male chimpanzees strive for is being on top, the one position where they will never have to grovel. It is the difficulty of getting there that induces aggression." Bonobos have been seen as sharply contrasting with chimpanzees, displaying female dominance over males, richly elaborated sexual behavior that often occurs in a nonconceptive context, and a general lack of aggressiveness. In de Waal's (1997:22) description, "Bonobo society, unlike that of chimpanzees, is best characterized as female centered and egalitarian, with sex substituting for aggression. Females occupy prominent, often ruling positions in society, and the high points of bonobo intellectual life are found not in cooperative hunting or strategies to achieve dominance but in conflict resolution and sensitivity to others." The importance of these closely related apes in the ontogeny of theories about the origins of human behavior cannot be overstated. Our understanding of the biology of extinct forms represented

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only by fossilized skeletal remains would be quite different if we lacked living individuals of *Pan* for comparison. Chimpanzees and bonobos provide us with examples of the range of possible adaptations for feeding, ranging, territoriality, mating, offspring rearing, and a variety of other behaviors without which there would be no starting point for reconstructing hominid societies. They are, because of their kinship with humans, their similar morphology, and their cognitive abilities, the main referential models for early hominids (Tooby and DeVore 1987). Wrangham and Peterson (1996) have recently argued for an evolutionary continuity of male violence that extends from our close ancestry with chimpanzees. They argue on behavioral and morphological grounds that humans have a greater phylogenetic affinity to chimpanzees than to bonobos.

In this paper I examine behavioral differences between chimpanzees and bonobos and argue that the social behavior of these two great apes, while distinct in some respects, is more similar than is often claimed. I use data from field studies of the two species to address interspecific differences in female dominance, sexual behavior, and male aggression.

Chimpanzee Social Behavior

The difficulty in generalizing about the natural history of *Pan troglodytes* is illustrated by the fact that the following two statements, either of which might be found in a textbook description of chimpanzee behavior, are equally accurate:

> A. Chimpanzee society is characterized by male control and dominance over females and by male aggression and sexual coercion directed at females. Male territoriality and patrolling exclude extracommunity males and acquire new females for male reproductive benefits. Females are essentially reproductive commodities over which males compete.
>
> B. Chimpanzee society is characterized by actively mate-soliciting females that incite male competition during their periovulatory period and that with their infants form the nuclear units of the social system. Females forage solitarily to optimize food intake in fruit patches and become more social when it suits their reproductive tactics. Males may appear to dictate mating efforts, but the promiscuous, mate-soliciting female is the driving force in the mating system of the species.

Female chimpanzees are indeed active mate solicitors, play important dominance roles in chimpanzee society, and strongly influence the shape of the social system through their frequent sociality and periodic multiple matings. Few observers have observed wild chimpanzees, however, without concluding that females live in a largely male-dominated and male-controlled social environment.

Chimpanzees have been more intensively studied than bonobos, with several long-term (ten-plus years) and numerous shorter field studies. The study sites from which data in this paper are drawn are Gombe National Park, Tanzania (Goodall 1986), Mahale National Park, also in Tanzania (Nishida 1990), Taï National Park in Côte d'Ivoire (Boesch and Boesch 1989, Boesch 1994), and Kibale National Park, Uganda (Wrangham, Clark, and Isabirye-Basuta 1992, Chapman, White, and Wrangham 1994).

Our current view of chimpanzee society has emerged slowly, mainly because of the difficulty of obtaining a clear portrait of their fission-fusion form of polygyny. Increasing knowledge and changing attitudes about chimpanzee society can be divided into three stages, each corresponding to a decade of field research. During the first stage of modern primate research in the 1960s, chimpanzee behavior first became a subject of systematic field study. After several years of observation in the wild, Goodall (1968) had made the landmark discoveries of meat eating and tool use. Throughout the 1960s Goodall believed that chimpanzee society, unlike that of other group-living primates, had no group structure whatever. Relationships among individuals appeared to be in constant flux. Nishida (1968) was the first to put forward a model of chimpanzee society based on the "unit-group" (later called the "community" by Western primatologists). This large-scale structure has a stable membership but no stable grouping patterns other than mothers and their dependent offspring. Other members come together and depart unpredictably, giving rise to the label "fission-fusion society" (taken from Kummer's [1968] study of *Papio hamadryas*). Males tend to be social with each other, and male alliances play a crucial role in the maintenance of territorial borders and in attempts to control females.

In the second stage of research, in the 1970s, there were two major advances. The ecological influences on chimpanzee behavior became clear, and key aspects of their behavior that had previously been unsuspected came to light. In both Mahale National Park and Gombe National Park, the negative effects of artificial provisioning, which had led to heightened intracommunity aggression, were recognized and curtailed, and the collection of data became more systematic and included more ecological information. At Gombe, observation of the animals during long follows through the forest began to replace data collection in the feeding station. Wrangham (1979) conducted the first thorough study of chimpanzee behavioral ecology, focusing primarily on the males. It was this study that developed Nishida's idea of the community as a male-defended structure within which less sociable females traveled alone to optimize their use of food patches. Later observation of intercommunity lethal territoriality reinforced the view that chimpanzee society was male-controlled from both within and without. This represented a fundamental change in thinking about chimpanzees and also a revelation for its similarity to the homicidal aggression that is a regular feature of many human societies. Meanwhile, life histories of females showed that they typically emigrate from their natal communities at or after puberty (Goodall 1986). Female reproductive strategies involve multiple matings with males of their own and other communities. Despite Goodall's early observations of intensely aggressive competition among males for estrous females, chimpanzee social systems came to be described in terms of casual promiscuity.

In the third stage of chimpanzee field research, from the early 1980s through the 1990s, the diversity of chimpanzee behavior became clear as studies from different regions of Africa began comparing research findings on tool use (McGrew 1992), hunting styles (Boesch 1994, Stanford et al. 1994*b*), and feeding ecology (Chapman, White, and Wrangham 1994). Two further long-term field studies produced new perspectives on tool use, hunting, and social cognition (Boesch and Boesch 1983, 1989; Chapman, White, and Wrangham 1994). Ecological data on food patches and their utilization led to predictions that explained the variation in party size and cohesiveness between the major study sites. Chimpanzee populations exhibit considerable cultural variation (McGrew 1992), with learned group traditions that parallel traditional human societies technologically. This emerging realization has made it clear that the extermination of a chimpanzee population represents the permanent loss of any traditions that were unique to those animals.

Party size in chimpanzees appears to be a function of both food-patch size and distribution and the presence of sexually receptive females (Goodall 1986, Wrangham, Clark, and Isabirye-Basuta 1994). At Gombe, Goodall (1986) considered females with sexual swellings to be the primary attractant influencing the formation of large mixed-sex parties. She noted that years in which many females were cycling were also the years of largest mean party size. Stanford et al. (1994*b*) also found a significant positive correlation among Gombe chimpanzee party size, the presence and number of swollen females, and the tendency to hunt. Most published papers suggest that party size is primarily a function of food availability (White and Wrangham 1988, Chapman, White and Wrangham 1994). Data on female cycles in relation to fluctuation in party size from various chimpanzee study sites are critical to testing this hypothesis.

Social relationships between the sexes vary among the best-studied chimpanzee populations, and there has been some disagreement about the nature of chimpanzee community structure. Gombe foraging parties are small (fig. 1) relative to those at other sites. At Taï, Boesch (1991) argued that large party sizes were a response to the threat of predation by leopards. He also argued that the social system of Taï chimpanzees was more of a bisexually bonded community than other chimpanzee populations (Boesch 1996). Recently, Doran (1997) has disputed both of these claims, using Taï data from a different period that showed community structure and party sizes essentially the same as for other well-studied chimpanzee populations. At Gombe, Wrangham (1977) considered individual female home ranges as somewhat independent of the male community structure; centrally located females were thought to be core members of the Kasakela community, while more peripheral-ranging females might have membership in the neighboring community as well. Goodall (1983) pointed out that females are wary of the males of neighboring communities, suggesting that they cannot travel with impunity between adjacent male kin groups and may suffer severe, even lethal attacks from stranger males when ambushed in territorial overlap zones. Male chimpanzees remain in their natal community and join groups of males as they approach maturity (Goodall 1986). These male groups tend to be highly related (Morin et al. 1993). They patrol territorial borders and attack all extracommunity individuals encountered except for reproductively fertile females, whom they attempt to recruit into their own community (Goodall 1986, Nishida 1990). Females, meanwhile, transfer between and may even belong to multiple communities, being allowed to do so when they possess sexual swellings. Recent data from Taï National Park show that females may reside in one community but mate and conceive offspring with males from another community (Gagneux, Woodruff, and Boesch 1997). This suggests that chimpanzee mating systems and social systems are not necessarily the same.

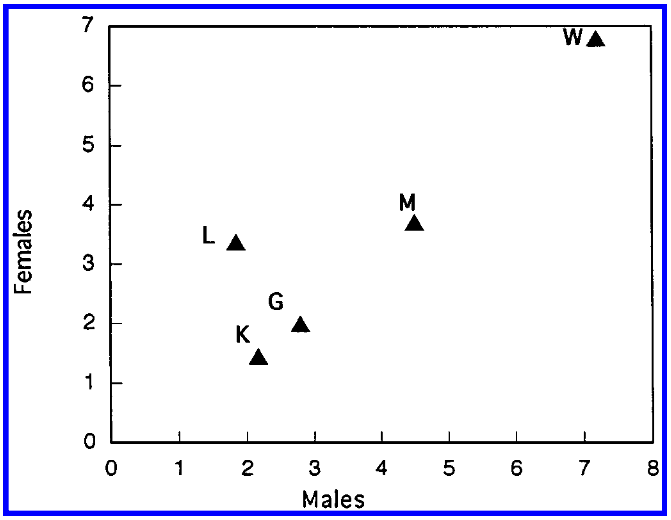

FIG. 1. *Mean number of adult males to adult females in foraging parties for chimpanzees and bonobos.* P. paniscus: W, *Wamba;* L, *Lomako.* P. troglodytes: G, *Gombe;* K, *Kibale;* M, *Mahale.*

Bonobos

For many years bonobos occupied a dimly understood place in the biology of the great apes because of the lack of captive or field studies, and they were necessarily ignored in reviews of great-ape behavior. Even a recent review of great-ape reproductive behavior (Nadler 1995) omitted bonobos, referring repeatedly to the gorilla, orangutan, and chimpanzee as "the three great ape species.'' Bonobos were known as pygmy chimpanzees in earlier descriptions, and morphological studies that compared them with chimpanzees were undertaken decades before any behavioral information became available. In the 1970s these morphological studies began to focus on shared traits of the bonobo, chimpanzee, and humans. Zihlmann and Cramer (1978) described morphological distinctions between bonobos and chimpanzees, and Zihlmann et al. (1978) put forward the bonobo as the best model for earliest hominid functional morphology and behavior because of evidence of retention of early-hominid-like traits. Zihlmann's bonobo model was met with skepticism on the grounds that the bonobo might be an ecologically and morphologically divergent chimpanzee rather than having traits homologous with earliest hominids (Latimer et al. 1981, Johnson 1981).

Bonobo behavior is well-known only from two field sites in central Congo, Lomako (Badrian and Badrian 1984; White 1988, 1996*a, b;* Hohmann and Fruth 1993, 1994) and Wamba (Kano 1983, 1992). In the early 1970s, researchers conducted surveys of bonobo populations in Congo that led to the establishment of these two sites. These sites continue to produce the bulk of field data, with Wamba, under the direction of Takayoshi Kano, producing especially detailed observations of sociosexual behavior and intracommunity social dynamics (Kano 1983, 1992; Furuichi 1987, 1989; Idani 1991; Hashimoto and Furuichi 1994). Lomako has produced detailed studies of social behavior and behavioral ecology, with an emphasis on the latter (Thompson-Handler, Malenky, and Badrian 1984; White 1988; White and Burgman 1990; Malenky and Stiles 1991). The difference in research foci may be due to differences in habituation. At Wamba, bonobos have long been habituated to observation in an artificial sugarcane plantation, while at Lomako no provisioning was used and the animals were less observable for many years. Less intensively worked bonobo research sites have been established at Yalosidi (Kano 1983) and Lilungu (Sabater Pi et al. 1993).

Like chimpanzees, bonobos eat mainly ripe fruit, supplemented with herbaceous terrestrial plants. Wrangham (1986) has suggested that bonobos, lacking food competition with gorillas, have adopted a diet high in widely available pithy foods to mitigate the risk of fruit patchiness. Bonobos live in fission-fusion polygynous societies, the territories of which are defended by strongly male-philopatric kin groups. Bonobo foraging parties form for the apparent purpose of providing females with optimal fruit-foraging opportunities (Kano 1992). Bonobo foraging parties tend to be substantially larger than those of chimpanzees, though there is considerable size overlap between the species among different study sites. The smaller party sizes seen in chimpanzees appear to be related at least partially to differences in food-patch size and distribution and to bonobo use of herbaceous groundcover plant foods in addition to fruit. Whether the food-patch sizes that allow bonobo parties to be larger is a spatial difference (Malenky and Stiles 1991) or a temporal one (Chapman, White, and Wrangham 1994) is unclear.

Female bonobos emigrate from their natal community at or near sexual maturity and establish themselves in neighboring-community ranges (Idani 1991). Furuichi (1989) found that immigrant female bonobos established bonds with one female at a time and slowly become central in their new communities. He found that the oldest females tended to be the highest-ranking. Idani (1991) and Kano (1992) reported that most transferring females were nulliparous and that they established bonds with females that were unrelated to them. Female-female bonds are thus based on patterns of affiliation but not necessarily on kinship.

Male bonobos are strongly philopatric, but this philopatry is not accompanied by territorial aggression as consistently intense as in chimpanzees. Both hostile and peaceful intercommunity encounters are seen, and copulation between females and extracommunity males has been reported (Kano 1992). It would be wrong, however, to characterize bonobo communities as coexisting peaceably, since half of encounters do involve aggression of some sort (Kano 1992). Chimpanzees were observed for more than 15 years and thousands of observer-hours, including many intercommunity encounters, before lethal aggression was seen. We should therefore not assume that lethal or injurious intercommunity aggression never occurs among bonobos. Lethal aggression during chimpanzee intercommunity encounters has been reported from Gombe (Goodall 1986), Mahale (Nishida 1990), and Kibale (Wrangham, personal communication). The all-male patrols that characterize chimpanzees are rarer among bonobos (Kano 1992), though as bonobo party sizes increase the percentage of the party that is male also increases (White 1988).

Bonobo-Chimpanzee Comparisons

A number of stark differences in social behavior between bonobos and chimpanzees have been reported. I examine the evidence for these differences below.

REPRODUCTIVE ECOLOGY

Female-female relationships and sexual behavior are perhaps the two most-discussed differences between the societies of bonobos and chimpanzees. Adult and adolescent females of the genus *Pan* are characterized by the vivid advertisement of their sexual receptivity with perineal swellings for a portion of their menstrual cycles. Ovulation in both species occurs at the end of the period of maximal swelling, just before the swelling begins to detumesce (Wallis 1992). Male chimpanzees are attracted to females with swellings during the entire duration of their maximal swelling, though there is great individual and age-related variation among females in the level of interest they receive from males (Goodall 1986). When female chimpanzees are swollen they become more sociable, attract males, and join mixed-sex parties that may comprise a majority of the community. These aggregations often stay together for days, the males dispersing once the female detumesces (Goodall 1986). Swellings are thus an important influence on chimpanzee grouping patterns.

While the length of the cycle varies among different populations of the two species (table 1), chimpanzees and bonobos are similar in the percentage of the menstrual cycle during which maximal swelling occurs. Wild female bonobos experience a period of about 14 days of a 42-day cycle during which their anogenital region is tumescent, pink, and highly visible to others in the community (Furuichi 1987). Longer swelling durations (up to 23 days) have been reported from captivity (Dahl 1986, Dahl, Nadler, and Collins 1991). Female chimpanzees are maximally swollen for slightly fewer days (mean = 13 at Gombe) of a shorter (36-day) menstrual cycle (Wallis 1997). At Gombe, although births are aseasonal (Goodall 1986), swelling cycles are seasonal, peaking in the dry season and influencing party aggregations (Wallis 1995). Whether olfactory cues accompany the visual stimulus of the swelling is unknown but strongly suspected. Female chimpanzees and bonobos also swell while they are pregnant or lactating, though these anovulatory swellings may be less regular in frequency and duration (Wallis 1992). Males are nevertheless attracted to nonovulating swollen females. Swellings during pregnancy and in adolescent females thus play a role in nonreproductive sex.

BONOBO SEXUALITY

It has become a fundamental premise of bonobo sexuality and of the bonobo's link to human behavior that among primates only bonobo and human females are sexually active outside the periovulatory period. In the wild, nearly all female chimpanzee sexual behavior is observed during maximal or near-maximal swelling (Goodall 1986). This has been considered in sharp contrast to the behavior of bonobo females, which are said to have been released from the constraints of reproductive sex and remain sexually receptive throughout the menstrual cycle (Nadler et al. 1991; Thompson-Handler, Malenky, and Badrian 1984). This nonconceptive sex has been considered an evolved mode of social communication (de Waal 1987, Wrangham 1993, Parish 1994). The most detailed study of sexual receptivity in wild female bonobos, however, does not support this claim. Furuichi (1987) found that although female bonobos at Wamba do copulate when not maximally swollen, more than 95% of matings were observed during periods of maximal or near-maximal swelling. This is approximately the same as for chimpanzees (97% [Goodall 1986]). Female bonobos are thus somewhat more flexible than other apes in the timing of sexual receptivity, but they are not released from the constraints of sexual swelling cycles.

Female bonobos are frequently portrayed as hypersexual, but mating frequencies in the wild are actually quite comparable for the two species of *Pan.* De Waal (1987) reported that bonobos in the San Diego Zoo copulated five times as frequently as chimpanzees, although he acknowledged that this rate might be an artifact of captive confinement. Comparisons between a wild and a captive population may not reflect naturalistic mating patterns. Swollen female chimpanzees copulate with multiple males during the early stages of their swelling cycle. As many as 50 copulation bouts with eight males in a day have been recorded, and swollen females have copulated with up to eight adult males in several minutes (Goodall 1986). At Wamba, bonobo females actively solicit sex from a range of males and may copulate multiple times per hour while swollen (Kano 1992). However, female chimpanzees at Mahale have higher reported mean copulation rates than Wamba bonobos (Takahata, Ihobe, and Idani 1996). Moreover, male copulation rates in the wild are higher among chimpanzees than they are among bonobos. Mahale male chimpanzees copulated at a higher mean rate than male bonobos at Wamba (*P. troglodytes* 0.20–0.29/hr., *P. paniscus* 0.10–0.21/hr.). These rates are for adults, but adolescent male chimpanzees also have higher copulation rates than adolescent male bonobos. Bonobo mating rates are therefore not higher than those among chimpanzees if the swelling duration and not the entire interbirth period is used as the time frame. If the entire interbirth period is included, then bonobos do show higher copulation rates, because the period of maximal swelling occupies a slightly larger percentage of the menstrual cycle in bonobos than it does in chimpanzees (Kano 1996).

Female bonobos do not mate more frequently or significantly less cyclically than chimpanzees, but there are some fundamental differences between the two species. One difference relates to the presence of swollen females in foraging parties. At Gombe, at least one estrous female chimpanzee is present in the community about half of all days (Tutin 1979). However, only a mi-

TABLE 1
Anogenital Swelling Durations in Chimpanzees and Bonobos

Mean Maximal Swelling Duration (days)	Species/Site	Source
13 (36.1% of 36-day cycle)	*P. troglodytes*/Gombe	Wallis (1997)
12.5 (39.7% of 31.5-day cycle)	*P. troglodytes*/Mahale	Hasegawa and Hirai-Hasegawa (1983)
14.6 (34.8% of 42-day cycle)	*P. paniscus*/Wamba	Furuichi (1987)
12.9 (39.3% of 32.8-day cycle)	*P. paniscus*/Wamba	Kano (1996)
23.5 (47.9% of 49-day cycle)	*P. paniscus*/captive	Dahl (1986)

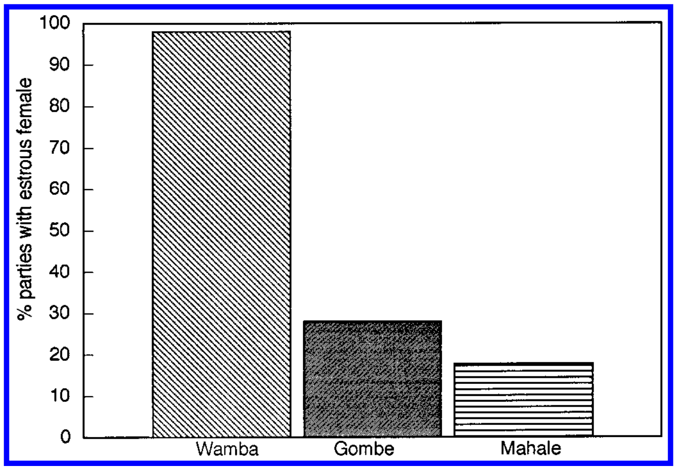

FIG. 2. *Percentage of foraging parties containing one or more estrous females, Wamba* (P. paniscus [*Kano 1992*]), *Gombe* (P. troglodytes [unpublished data]), *Mahale* (P. troglodytes [*Nishida 1968*]).

nority of mixed-sex foraging parties contain a swollen female (fig. 2; 20–30% for Gombe and Mahale). Moreover, the data presented for Gombe are somewhat inflated because the sample of parties used is drawn from hunting parties, which tend to be substantially larger than foraging parties on the whole (Stanford, unpublished). By contrast, nearly every mixed-sex party of bonobos has at least one sexually swollen female (98%, Wamba [Kano 1992]). This is because of the larger mean size of bonobo parties and the greater number of days on which each female is maximally swollen. The importance of this difference is that access to reproductively active females is much greater for bonobo males than for chimpanzee males, perhaps accounting for the lower levels of intermale aggression that are reported for bonobos.

BONOBO FEMALE DOMINANCE

Another reported difference between bonobos and chimpanzees involves the web of relationships among adult females and males. Chimpanzee society is male-dominated; adult males are typically dominant over all adult females, and adolescent males rise in rank by dominating each adult female before reaching the bottom of the male hierarchy (Goodall 1986, Nishida 1990). The overall level of affiliative behaviors such as grooming or support in conflicts is lower among chimpanzees than among bonobos, even among females whose infants may form play groups in their presence (Goodall 1986). It may be that female chimpanzees are affiliative with each other but that their bonds are less apparent than female-male and male-male ones. Eventually, female chimpanzees establish themselves as members of a new community, though many spend the majority of their time alone. Dominance relationships among female chimpanzees are often not obvious to an observer and may be nonlinear (Goodall 1986).

Female bonobos also transfer to new communities at adolescence and also may receive aggression from the females in the new community (Idani, cited in Furuichi 1989). Bonobo females are by contrast often dominant to males (Kano 1992) and form close relationships with males and especially with other females (Furuichi 1989, Idani 1991). The power base, which in chimpanzee society rests solidly with adult males, is therefore more female-centered in bonobos, perhaps because of greater bonobo female sociality that enables female coalitions to form and to dominate males (Furuichi 1989; Parish 1994, 1996). However, Wood and White (1996) have shown that at Lomako females are dominant only in the arena of feeding priority. Most sex-for-food exchanges among bonobos at Lomako occur just before males allow females priority of access to feeding patches, and this may be part of a larger pattern of strategic male deference in this species. If social dominance is considered separately from priority of feeding access, the pattern of dominance in bonobos more strongly resembles that of chimpanzees. Genital-genital rubbing is a nonreproductive sexual behavior of female bonobos and is a further example of affiliation among females. The primary goal of genital rubbing appears to be easing intracommunity tensions, particularly when competition over food threatens to disrupt social harmony (White 1988). Such affiliative encounters between females occur frequently in captivity as well (de Waal 1987; Parish 1994, 1996).

It is probably not true that male bonobos are not affiliative with each other; rather, their bonds may be less apparent and perhaps less strong than female-female and female-male bonds tend to be. Male bonobos engage in territorial defense (Kano 1992), and bonobo society is strongly male-philopatric. The emphasis on female sexuality and female power is the result of studies showing that of female-female, male-female, and male-male affiliation the last is least frequent.

MEAT EATING

Meat eating by chimpanzees is well documented (Teleki 1973; Takahata, Hasegawa, and Nishida 1984; Uehara et al. 1992; Boesch and Boesch 1989; Stanford et al. 1994*a;* Stanford 1998) and is a systematic aspect of chimpanzee behavior across their geographic range. Chimpanzees incorporate the meat of hunted mammals in their diet, and at some sites the biomass of the meat captured by a community may approach 1,000 kg per year (Stanford 1996). Red colobus monkeys (*Colobus badius*) are the main prey item at Gombe, Mahale, Kibale, and Taï. The impact that chimpanzees have on red colobus populations at these and other sites may be an important population regulator (Stanford 1995) as well as an influence on the structure of the red colobus social system (Stanford 1998). Captured meat is often shared among the hunting party and may be shared nepotistically and strategically. Most kills (approximately 92% at Gombe [Stanford et al. 1994*a*]) are made by males. Chimpanzees probably hunt for both nutritional and political reasons in that alliances are cemented by the giving of meat. They also appear to obtain meat for sociosexual benefits in that males sometimes offer meat to females and receive matings in the process (Nishida et al. 1992, Stanford et al. 1994*b*). Hunting at Gombe, Mahale, and Taï is seasonal, and at Gombe this seasonality corresponds with periods of the availability of swollen females that are a robust predictor of party size (Stanford et al. 1994*b*). At both Gombe and Taï, hunting success increases with increasing party size.

Among bonobos, meat eating is rare. Indeed, forest monkeys (*Cercopithecus* ssp. and *Colobus* ssp.), which would be relished prey for chimpanzees at Gombe, Mahale, Kibale, and Taï, have been used as playthings rather than as food items by bonobos at Lilungu (Sabater Pi et al. 1993). Wamba bonobos rarely hunt even though their mean party size is larger than that found in any chimpanzee population (Kano 1992). If male chimpanzees hunt primarily for political and sociosexual rather than nutritional reasons, then one might expect male bonobos to be less interested in hunting, for two reasons. First, female bonobos do not need to engage in political or sexual behavior to obtain a share of the meat; they may simply take it away. Hohmann and Fruth (1993) reported instances of females' taking fresh kills away from male captors, which occurs very rarely in chimpanzees. The manipulative use of meat seen in male chimpanzees would not be effective for male bonobos, since they typically defer to females in feeding situations. These observations point also to a social rather than nutritional basis for hunting in chimpanzees. Given that there is a range of potential prey, including monkeys, at both bonobo study sites, it is hard to understand why bonobos would show little interest in hunting if meat were the prized nutritional resource it has been thought to be in chimpanzees.

SEXUAL SWELLINGS

The sexual swelling is an evolved feature which, because it is visually obvious and connected to reproduction, has received much attention from primatologists. Although Lovejoy (1981) assumed that humans had evolved concealed ovulation as a reproductive adaptation by females, it is also possible that the *Pan* lineage evolved swellings to advertise ovulation from a concealed-ovulator ancestor. Although it exerts a major influence on chimpanzee and bonobo society, its function is not clear. Vividly advertised ovulation has arisen several times in the primate order, including among the ancestors of some cercopithecines, some colobines, and the Hominoidea (Sillén-Tullberg and Møller 1993). Hrdy (1981) and Harcourt (1981) have argued that sexual swellings may serve to confuse paternity and thereby increase a male's parental investment. The likelihood of aggression toward that female or toward her infant might also be reduced as a result (Takahata 1985). Since swollen female chimpanzees and bonobos transfer between communities and female chimpanzees that are encountered by stranger males are attacked and even killed if they are not swollen, the sexual swelling appears to allow female chimpanzees mobility between communities.

This hypothesis also addresses the object of male-bonded territorial defense in chimpanzees. The number of males in a community is positively correlated with the size of the territory that is defended against other communities (Stanford 1998). This male-bonded behavior may be related to either female defense or food defense; data on territoriality and female transfer are seen as key in modeling the behavior of the common hominoid ancestor (Ghiglieri 1987, Wrangham 1987). If female swellings are related to intense male territoriality because they grant the females safe passage between communities, then territoriality may be food-resource-based. This is because, from a male's perspective, having as many females as possible in the community should be a reproductive benefit, and so any immigrating female should be welcomed whether currently cycling or not. To resident females new immigrants represent both food and mating competition. Swellings may therefore allow female chimpanzees to enter communities against the wishes of previous immigrants because they do so at a time when their swellings make them highly attractive to males. The same may apply to female bonobos, which also face aggression from resident females when immigrating to a new community.

Conversely, Hamilton (1984) and Hrdy and Whitten (1987) have hypothesized that by signaling ovulation, genital swellings might increase paternity certainty and therefore paternal investment by males. Clutton-Brock and Harvey (1976) argued that because a swollen, ovulating female becomes a focus of excitement and competition among males, the swelling's function is to incite male competitive behavior, allowing her to choose the most fit mate or mates. Harcourt (1981) has suggested that the swellings may function simply to extend the time period during which females can locate and stay in proximity to potential male mates. Tutin (1979) reported, however, that most conceptions during her study of Gombe chimpanzee reproductive behavior probably occurred during consortships, outside of the polygynous setting for which Clutton-Brock and Harvey's "best-male" model predicts that swellings evolved. She also pointed out that the "best-male" hypothesis does not fit chimpanzee society well, since females choose mates on the basis of prior affiliative patterns with males who offered grooming and food-sharing opportunities. Reproductive benefits may accrue to them only indirectly through benefits to their offspring. More recently, Wallis (1997) has reviewed two decades of Gombe data on conceptions and found that the majority occurred in polygynous settings, not in consortships.

Explanations of the nature and origin of chimpanzee and bonobo sexual swellings seem to be based primarily on the premise that of the two species it is the latter that is the derived one. This premise may stem from bonobos' more limited geographic range and their elaborated sexual behavior. In addition, bonobos may tend to be viewed as the divergent form because they have been described and studied more recently. This premise may not, however, be warranted. For instance, implicit in the literature about bonobos is that females have extended the duration of the sexual swelling, the result of which is thought to be increased female cooperation and increased affiliation between males and females. Highly visible swellings are unique traits in this hominoid clade. However, since the ancestral behavioral patterns of chimpanzees/bonobos are unknown, it is also unknown whether swellings in bonobos have been elaborated and extended in duration through natural selection. Alternatively, female chimpanzees may have shortened swelling cycles as an adaptation to attract multiple mates while minimizing feeding competition. The latter is a reasonable speculation given the typically asocial foraging strategy of female chimpanzees and the number of food competitors in large mixed-sex parties alongside whom the swollen females must forage.

Goodall (1983) argued that females in each chimpanzee community belonged to one community only; they were wary of other community territories and might be ambushed while foraging in a territorial overlap zone. Wrangham (1979) argued that female home ranges were relatively fixed and that they might be part of more than one community over which the males ranged; the idea that males attempt to maximize territory size as a way to encompass more females' ranges for male reproductive advantages follows from this point of view. Data from some study sites tend to support Goodall's view; Hasegawa (1990) has shown that the concept of females and males occupying separate ranges is untenable for Mahale chimpanzees.

Influences on Our View of Great-Ape Societies

It is clear that much of the research on these two intensively studied apes remains fraught with untested assumptions. In the search for behavioral patterns that may be adaptations shared by humans and chimpanzees, the behavioral traits of chimpanzees and bonobos discussed here—hunting, reproductive behavior, mating systems—have been the most often mentioned. In this final section I consider some underlying influences that may help to account for the ways in which both primatologists and the public understand the societies of these two apes.

The primary reason for change in our ideas about great-ape societies over time is the accumulation of new data. Research findings and their interpretations are strongly influenced by the simple accumulation of knowledge about a species until a particular behavioral trend becomes evident or it becomes possible to reconcile a set of seemingly unrelated behavioral facts using a single paradigm. The paradigm formation may itself be subject to social influences, because research biases lead one to collect some types of data rather than others at different stages of the research history of a topic. However, it is especially the case in field primatology that the logistics of research, the longevity and extended ontogeny of the subjects, and the importance of documenting the life histories of many individuals of all age- and sex-classes contribute substantially to a growth of ideas in the discipline through cumulative normal science. Considering chimpanzees to be entirely promiscuous without any definable social system was a result of the difficulty in documenting rare events: female migrations, intercommunity conflicts, hunting and meat sharing, male dominance upheavals. Changing this view took more than a decade; as data accumulated so did the depth of the portrait of chimpanzee society. The number of observer-hours spent with bonobos in the wild is still comparable to the time spent watching chimpanzees in the 1960s. Comparisons between chimpanzees and bonobos therefore suffer from the scantiness of the data on bonobo behavior, allowing interpretations based more on perceived contrasts with chimpanzees than on observational evidence from bonobos. While the evidence for chimpanzee behavior may be subject to interpretation, there can be no questioning the fact that hunting is a primarily male activity, that lethal aggression occurs between communities, and that these are characteristic of chimpanzees in the wild across the African continent. The history of primatology has been composed of a series of new paradigms to explain accumulating new data. These often involve dichotomies that are shown later to be false; for example, the male-philopatric versus female-philopatric dichotomy has been called into question (Moore 1984*a,* Strier 1994). Such models tend to be predictive for a time, but as new, contradictory data accumulate they become obsolete. The dichotomy currently drawn between the social systems of chimpanzees and bonobos may not accord well with field data.

Second, although many of the most detailed studies of intragroup social dynamics among living primates come from captive colonies, captive behavior frequently differs from behavior in the wild. In the case of bonobos, early captive studies demonstrated behaviors that became the focus of much public and scientific attention (e.g., de Waal 1987). Bonobos engage in a rich array of sociosexual behaviors in the wild, but the frequency of the behaviors is much lower than in captivity. Captivity produces heightened frequencies of many behaviors for a variety of reasons, among them release from the need to forage, greater opportunities for social interaction, and enforced proximity and boredom. Orangutans are, for example, highly sociable in captivity relative to their solitary wild counterparts. While there is much to be gained from the captive study of behaviors that are impossible to record well in the field, biases are introduced into our interpretation of species-typical behavior because of the way in which captivity influences behavior.

Third, contextual biases may emerge from the circumstances in which the research is done. They represent the situating of ideas and interpretations of evidence in terms of the perspective the researcher brings to the research. These influences are pervasive (though whether they fundamentally change the doing of science is open to debate). The behaviors at the heart of the chimpanzee-bonobo interspecific variation—sexuality, power and dominance, aggression—are those that also lie at the center of the debate about human gender issues and what molds our own behavior. Ortner's (1974) argument that men are to women as culture is to nature may be reflected in a more recent version that is evident in popular-scientific portrayals of these two apes: chimpanzees are to bonobos as men are to women. A recent account of the evolutionary continuity of human violence from an ape ancestor makes a strong case for chimpanzees as the referent models for the behavior of modern human males (Wrangham and Peterson 1996). Murder, sexual coercion, hierarchy, and striving for status are all traits that Wrangham and Peterson ascribe to chimpanzees as well as to human males. De Waal's recent (1997) account of bonobos ascribes to them characteristics often used to describe women: nonaggressive, sensual, power-sharing, strong through alliances rather than individually. He writes, ''The chimpanzee resolves sexual issues with power; the bonobo resolves power issues with sex'' (p. 32). While these characterizations are based on observational data, they may also be influenced by views of the two apes that accord with human male and female gender stereotypes. These stereotypes are influenced by the public's desire for explanations of the roots of human behavior. This issue has risen to enough prominence that the newsletter of the American Anthropological Association recently devoted a series of columns to the treatment of biological anthropology by the media. The portrayal of humans as at an evolutionary crossroads, able to choose the bonobo's sensuous ''Make love, not war'' nature or the chimpanzees warring, status-striving nature, finds an eager audience. Whether current images of chimpanzee and bonobo societies and the dichotomy between them accord well with field data remains for future fieldwork to determine.

Comments

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In the same way that paleontologists prefer their fossil finds to belong to a human ancestor rather than to an extinct side-branch, experts on ape behavior like to claim that their subjects are the only or best model of the last common ancestor, Chimpanzee researchers are used to this situation, routinely describing the chimpanzee as humanity's closest living relative. There exists another relative, however, that is equally alive, equally close, and equally relevant to an understanding of human evolution. While this has delighted some, it obviously disturbs others.

Two strategies have emerged to keep bonobos at a distance so as to preserve chimpanzee-based scenarios of human evolution, which traditionally emphasize warfare, hunting, tool use, and male dominance. The first strategy is to describe the bonobo as an interesting but specialized anomaly that can be safely ignored as a possible model of the last common ancestor (see Wrangham and Peterson 1996). The second strategy, adopted by Stanford, is to minimize the differences between the two *Pan* species: if bonobos behave, by and large, like chimpanzees, there is no reason to question the latter species's prominence as a model. Let me review the factual basis of some of Stanford's similarity claims:

Rate of sexual behavior. In arguing that the rates of sexual behavior in bonobos and chimpanzees are similar, Stanford counts only copulations between males and females. This is indeed the bulk of sexual activity in the chimpanzee, but the bonobo has sex in virtually all possible partner combinations: male-female sex is not even the most common pattern. Genital rubbing among females, the most typical pattern of the species, is absent in chimpanzees. This pattern is conveniently ignored in the calculations. Including all sexual encounters, I have reported a much higher interaction rate among bonobos than chimpanzees (de Waal 1995 and fig. 1).

Effects of captivity. The argument that the high rate of sociosexual activity in captive bonobos might be attributable to confinement fails to consider that the above comparison is not with wild chimpanzees but with captive ones. Why are chimpanzees not similarly affected by confinement? Only captive studies control for environmental conditions and thereby provide conclusive data on interspecific differences; field studies usually concern different species under different ecological conditions.

Peacefulness. Given our current knowledge, it is entirely correct to describe bonobos as relatively peaceful. In captivity, bonobos show less violence and considerably higher rates of reconciliation following fights than chimpanzees. Bonobos are by no means lacking in aggression, however, and despite their reputation they are actually less tolerant in relation to food than chimpanzees (de Waal 1992). In the field, lethal intercommunity aggression, forced copulation, and infanticide have never been observed. Stanford is not the first, however, to warn that such behavior may yet be discovered (de Waal 1989:221).

Female dominance. If a male chimpanzee chases a female away from his food, we generally attribute this to his dominance. This rule has been followed by ethologists for every species on the planet, but now we learn that female bonobos ''are dominant only in the arena of feeding priority.'' It is claimed that if we look beyond feeding priority the relations between the sexes in bonobos and chimpanzees are more similar. This is based on a study by Wood and White (1996) that failed to iden-

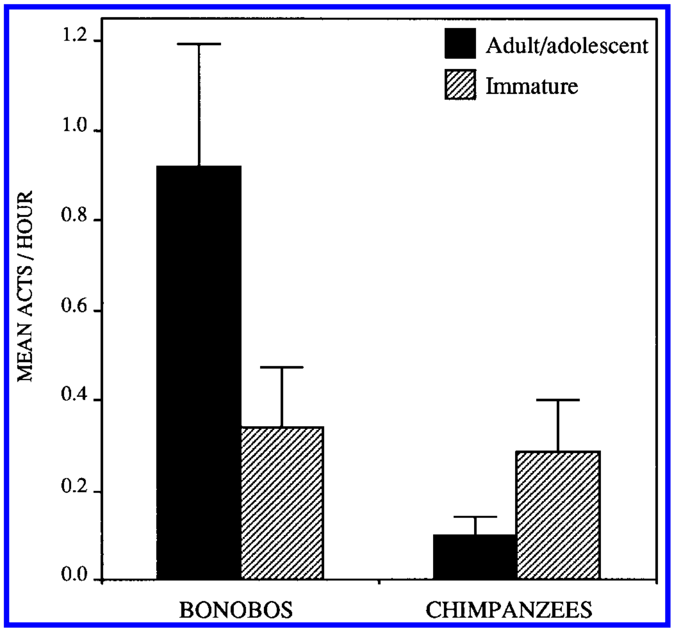

Fig. 1. *Mean (+ SEM) number of sociosexual acts initiated per hour per individual for the San Diego bonobos and an outdoor colony of chimpanzees at the Yerkes Primate Center's field station, separately for adults and adolescents (*black*) and younger individuals* (hatched). *The adult rate was significantly higher in the bonobo group despite a reduced number of available partners compared with the chimpanzee group. The juvenile rates of the two species did not differ. From de Waal (1995).*

tify male and female bonobos individually; possibly some males in this community were able to chase some females and did so frequently, but a pooled analysis would show the class of males dominating the class of females. Other investigators of the same community did achieve individual recognition and claim obvious female dominance (Fruth and Hohmann, cited in de Waal 1997:79–80). Similarly, at another bonobo field site Furuichi (1997) noted that the alpha female could chase high-ranking males and that the alpha male sometimes retreated for low-ranking females. Furthermore, in all captive groups that I know female bonobos dominate males—an enormous contrast with chimpanzees (e.g., Parish 1994).

Finally, when Stanford speculates about the sociocultural context of the current fascination with bonobos, it would be good to include an analysis of why it has taken so long for scientists to discuss the matrifocal nature of bonobo society and the species's rich sexuality. It is no accident that the first time Frans Lanting and I worked together on an illustrated account of bonobo society we did so for *GEO Magazine;* U.S. publishers panicked at the thought of a full story. Rather than concluding that the bonobo seems a species made for the media, the question is really what has hampered its unique social features from surfacing and why attempts are still being made to push it to the sidelines. Anyone interested in the reconstruction of our evolutionary past will need to face the implications of having a sexy, female-centered close relative.

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Stanford is to be congratulated for his attempt to focus on the similarities rather than on the differences between chimpanzees and bonobos. I agree that the emphasis so far put on the behavioral dichotomy between the two *Pan* species may be due to the relatively briefer study of bonobos from only two major sites compared with the longer-term investigations of many study sites of chimpanzees. Nevertheless, the combined data set of only these few studies, mostly at Wamba and Lomako, allows Stanford to place the bonobo within the behavioral range of chimpanzees. He excuses the remaining behavioral gaps between the *Pan* species by a lack of published data from the wild and ends his comparison with an appeal for future field research to seek data that will eventually allow systematic treatment of the apparent dichotomy. However, published literature is already available that would allow some of the gaps to be filled and would make his point even stronger.

Discussing the differences in meat eating between the two *Pan* species, Stanford argues chimpocentrically, as if blinded by the quantity and quality of *Pan troglodytes*'s favourite prey, red colobus monkeys. This is almost as if a Texan consuming a T-bone steak daily were to consider a Bavarian savoring a pork roast on Sundays a vegetarian because it was pork instead of beef and because it was consumed only occasionally. At Lomako, *Pan paniscus* regularly kills and eats adult duikers, *Cephalophus* spp. (Hohmann and Fruth 1993, 1996). Admittedly, the amount of animal prey killed and eaten by bonobos at Lomako is not comparable to that recorded for chimpanzees, but whether meat eating has nutritional or social significance has yet to be clarified. The smaller the amount of a nonetheless regularly consumed food item the more it might be compensation for a nutritional deficit (such as trace elements) or self-medication (Huffman 1997).

If sharing fulfills a political function, the shared item need not be meat. At Lomako fruits such as *Treculia africana* or *Anonidium mannii,* weighing on average 10–15 kg, are regularly shared by bonobos (Hohmann and Fruth 1993, 1996)! They are seasonally available and during that time make up much of the daily diet. Again, their nutritional value can be disputed but their the social value cannot. Therefore, Stanford's interpretation of the apparent missing need for social or political ceremonies in bonobos, drawn from the low frequency of consumption of animal prey, seems misconceived. Perhaps he takes a typically male view of politics. Is it so hard to imagine that female bonobos might hunt, kill, and share for reasons similar to males'?

At Lomako, female bonobos hunt, possess, and distribute meat. Between 1990 and 1997 we saw seven cases of the sharing of a captured duiker, all but one of which were adult. Each time, females had possession of the carcass and shared mostly with other females; males only occasionally got a share. The rate of fruit sharing was 15 times greater than that of meat, and again it was almost always females that owned the food and controlled its distribution.

Cooperation by unrelated individuals and the resulting control of key resources is not self-evidently sex-biased in a male-philopatric society. Bonobo females cooperate, and the frequent sociosexual interactions that occur during these sessions may reinforce their political ties as well as the act of sharing itself. Instead of asking why bonobos are not avid meat eaters, perhaps we should ask why chimpanzees share only meat.

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Stanford presents a timely and needed discussion on the use of chimpanzees and bonobos as referential models for understanding the evolution of human behavior, questioning some of the generalizations that have been made about these species. Perhaps one of the most important points to take away from this article is the difficulty of generalizing about either chimpanzees or bonobos at all. What has become clear from research over the past few decades is the variability of behavior within the genus *Pan,* both geographically and temporally. As Stanford says, some of this is clearly the result of the changing focus of research questions, the gradual build-up of observations of infrequent behaviors, and differences in habituation, but it is also important to keep in mind the adaptability of chimpanzees and bonobos to changing ecological and demographic conditions. The social structure of a community may truly be different when examined over a long period of time.

Because our understanding of chimpanzee and bonobo behavior will change as our information increases, it is critical that we utilize the most up-to-date and accurate information when attempting to generalize or develop models. One aspect that is frequently misrepresented has to do with levels of habituation and the extent of artificial feeding at research sites. Stanford says that "at Wamba, bonobos have long been habituated to observation in an artificial sugarcane plantation." While this is true, it suggests that all observations at Wamba have been conducted under artificial feeding conditions, which is *not* true. Three unit-groups (E1, E2, and P) are well habituated to human observations whether in the forest or in an artificial feeding site. During the past decade or more, researchers at Wamba have consistently conducted observations away from artificial feeding sites, following the bonobos throughout the day in various parts of their range (Hashimoto and Furuichi 1994, Ihobe 1992, Ingmanson 1996, Ono-Vineberg 1997). In addition, it has also been possible to observe neighboring unit-groups (K, S, B) for short periods of time, providing comparisons between well-habituated groups and those that were less so. One clear difference I observed was that poorly habituated groups spent considerably more time in the trees, both for traveling and for resting, than did habituated groups, which frequently rested, groomed, played, and moved on the ground.

Stanford's statement concerning the defense of territory by bonobos at Wamba also needs examining. The unit-groups there do not have exclusive ranges. For example, in 1990–91 the E2 group ranged over approximately 45 km^2 (Ingmanson 1996), about half of which was also utilized by neighboring unit-groups—E1 on the south, K on the east, S on the north, and B on the west. Only a central part of the range was used exclusively by the E2 group during that period of observation. Intergroup interactions occur in these regions of overlap. A unit-group may defend a feeding spot on a particular day, using extensive vocalizations and intimidation displays, but it may also settle down after some time and feed side by side with the neighboring unit-group. In October 1990 this occurred almost daily between E2 and K (Ingmanson, unpublished data). The S group could always displace the E2 group, again making generalizations difficult, but this is clearly *not* territorial defense in the traditional sense used by most primatologists.

I agree with Stanford that "it is probably not true that male bonobos are not affiliative with each other." I have, in fact, observed frequent grooming between males, especially in the E2 group. It was possible to recognize affiliations between pairs of males based on grooming and proximity that remained the same between 1987 and 1991. This is the kind of behavior, though, that requires extensive observation away from feeding sites to elucidate.

Stanford notes that hunting by bonobos may be less frequent than hunting by chimpanzees because female bonobos have greater control of food resources. This control can clearly be seen in cases where predation *has* been observed (Ingmanson and Ihobe 1992). When a high-ranking adult female of the E2 group captured a flying squirrel, she proceeded to share it with other adult females and their offspring. None of the carcass went to any of the adult males, however, even though the highest-ranking male of the group had a temper tantrum on a branch below the feasting females.

A great many inaccuracies have crept into the realm of "common knowledge" concerning both bonobos and chimpanzees. These are maintained by referring only to early studies or captive data, both of which may give false impressions. The media and popular writings are particularly bad about this, but scientists are not immune, as can clearly be seen in the treatment of bonobo sexuality. Bonobos *do* engage in extensive sexual behavior, though recent field studies suggest that the difference from chimpanzees in this regard may be less than previously thought. From my own observations of both chimpanzees and bonobos under both field and captive conditions, where a chimpanzee will predictably use aggression in a situation a bonobo will use sex. Bonobos do engage in aggressive behavior, though, and chimpanzees do seem to use sexuality to manipulate social situations. The *emphasis* on the kind of behavior, I believe, differs between the two species. What bonobos are particularly good at is coordinating group activities, from feeding to travel, and sex, as well as communication, is a part of this. We must keep in mind that what *Pan* offers us is examples of the range of possible adaptations for an intelligent hominoid while we attempt to maintain scientific objectivity in our interpretations.

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Stanford has presented a good review of the behaviors of wild chimpanzees and bonobos and concludes that they are similar behaviorally. I too have argued that they have basically similar social systems of fission-fusion multimale polygyny and female dispersal. However, I disagree with Stanford on several points and still see a behavioral dichotomy between the two species of *Pan.*

Male-female dominance. At both Wamba and Lomako, females are dominant in the feeding context; females frequently supplant males while the reverse occurs much less. Stanford argues that the pattern of dominance in bonobos resembles that of chimpanzees if social dominance is considered separately. Priority of access to food is, however, an important function of dominance. Since most dominance interactions and virtually all agonistic episodes between adult females and males occur in feeding contexts, I find much less meaning in dominance occurring in the non-feeding context. Moreover, there is no difference between feeding and non-feeding dominance relationships among the bonobos of Wamba. For example, approaches of dominant females often give rise to submissive reactions by grooming males such as grinning, bending away, etc.

Copulation rate. Stanford stresses that, according to Takahata et al. (1996), both adult females and males at Mahale copulate at a higher mean rate than do those of Wamba. For bonobos, Takahata et al. used the data from the E1 group after the fission of the E group into E1 and E2. The copulation rate for each bonobo in the E1 group had dropped dramatically after this fission, possibly because of the decrease in group (community) size from 72 to 30. The Mahale M group consisted of about 100 chimpanzees. Stanford needs to address the possible effect of differences in group size for this point to be clarified.

Intergroup relationships. I think the most marked social difference between the two *Pan* species lies in intergroup relationships. A variety of intergroup affiliative interactions such as copulation, greeting, grooming, and social play are observed during the encounters of the E1 group with the P, E2, and B groups at Wamba. In contrast, often lethal aggression characterizes intergroup relationships in chimpanzees. Stanford argues that there may be lethal or injurious intergroup aggression in bonobos as well, since chimpanzees were observed for more than 15 years and thousands of observer-hours before lethal aggression was seen. This may indeed be so. I once found a severe laceration on the foot of a young adult male of the E1 group on his rejoining the main party after days of separation that might have resulted from intergroup aggression. However, the presence or absence of lethal intergroup aggression does not count for much, as the overall peaceful nature of bonobos is much more important in the social comparison between the two species. Are there any comparable observations of intergroup affiliative interactions in Gombe chimpanzees during the thousands of observer-hours before and after the first observation of intergroup killing?

Infanticide. Infanticide, on which Stanford makes little or no comment, is another important issue if social characteristics are to be compared between the two species of *Pan.* An infrequent but regular behavior in chimpanzees, it has been explained from the viewpoint of male reproductive strategies; male chimpanzees are said to kill infants to decrease the genes of extragroup males and simultaneously to induce estrus in females. There is no observation of infanticide in bonobos. Moreover, adult bonobo males at Wamba carry infants for short times on occasion, and infant carrying and care are exhibited even by adult males of different groups. The mothers of such infants do not respond nervously to these males. It is indeed difficult to conclude that infanticide does not exist in bonobos, but the observations so far indicate that, if it occurs at all, it is much less frequent than in chimpanzees.

Prolonged mother-son relationships. Bonobo males maintain close and intimate associations with their mothers throughout their shared lifetimes. The strong and prolonged mother-son bond is one of the most important social features in bonobos since it influences male dominance and, to some extent, interrupts the rigid male-male bond that is a major social trait in chimpanzees. This point also is not addressed by Stanford.

As I have shown here, bonobos show some marked contrasts in social features with chimpanzees. The interspecific differentiation in social influence by either sex is well reflected in these social differences: females are more influential in bonobo society and males more influential in chimpanzee society. This dichotomy is not influenced by popular wishes as Stanford argues but comes from direct field observations.

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Jane Goodall once said that we will not understand the real differences between chimpanzees and humans until we first accept their many similarities. The same argument applies to chimpanzees and bonobos, as admirably advanced by Stanford, but the case is even stronger than he states.

Ecologically, *Pan paniscus* is not confined to rain forest but like *P. troglodytes* also ranges into woodland savanna, as shown by recent field research in Congo (108′ 48″ S, 21′ 20″ E) by Thompson (1995). Further fieldwork will likely yield even more ecological diversity in the range of bonobos.

Reproductively, it is not clear that there are *any* differences within or across populations or species of *Pan* in length of menstrual cycle or proportion of the cycle taken up by maximal swelling (Takahata et al. 1996). All of the apparent variation in Stanford's table 1 could be due to sampling error: Kano's (1996) mean length of 33 days and Furuichi's (1987) of 42 days for bonobos at Wamba come from *N*'s of only 8 and 6 cycles. Other sources of variance include whether cycles of immature, aging, or pregnant females are part of the calculations. The only statistically proven species or population difference in cycle length comes from sample sizes of only 4 *P. paniscus* and 9 *P. troglodytes* in captivity (Dahl, Nadler, and Collins 1991).

Hierarchically, is there any convincing evidence of female dominance over males in nature outside of the distorting content of the artificial feeding area? (The Wood and White [1996] reference cited is only an abstract, so the data are not available for scrutiny.) Description of the primary goal of genital rubbing as the easing of intracommunity tensions seems to be a remarkably public-spirited interpretation of what is usually thought of as a self-serving act.

It is hard to know what to make of meat-eating rates at Wamba if most of the data come from the artificial provisioning area. Until day-long follows of focal subjects are reported for bonobos, it is hard to compare their hunting with that of well-habituated chimpanzees at Gombe, Mahale, or Taï.

If hunting is important to understanding the social behavior of *Pan* spp., then so too is elementary technology. Both involve social learning and food sharing. Here a stark difference between *P. paniscus* and *P. troglodytes* does emerge: Neither behavioral nor archeological data from wild bonobos show them to be tool users of any note. They show no subsistence technology (Ingmanson 1996). In contrast, all long-term studies of chimpanzees (including Bossou, not cited by Stanford) show varied tool kits that range in function from food getting to communication (McGrew 1992). This may be the crucial difference between these two sibling species.

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The close genetic relationship between chimpanzees, bonobos, and humans and, of all extant apes, their unique suitability as possible analogues for some stage of protohuman evolution (Milton 1987, Milton and Demment 1988) make speculations about their social behavior particularly compelling. Information on either species is far more likely to provoke interest and discussion in academic and popular circles than, for example, comments on the social behavior of the potto. As Stanford points out, there is also a tendency to try to mold our perceptions of the behavior of these two apes into models of what we view as ''most proper'' for human ancestors. Those who prefer a peaceable kingdom lean toward the image of the female-empowered ''Make love not war'' bonobo, while those inclined more toward ''Nature red in tooth and claw'' embrace the image of the male-bonded, predatory, and aggressive chimpanzee. Stanford suggests that some features of the social behavior of these two ape species may be more similar than has been appreciated—the emphasis on one or another of these postulated interspecific differences hinging, perhaps unconsciously, on the appeal of one or the other image as a more satisfactory or politically correct ancestral model for our own genus and species.

In this context, it is worthy of note that a somewhat similar situation exists in terms of some features of the social behavior of wild spider monkeys (*Ateles* spp.). Like chimpanzees and bonobos, all spider monkey species show a fission-fusion pattern of social organization. However, study of *A. paniscus* in Surinam showed that adult males were almost invariably encountered in subgroups with adult females and immatures rather than in all-male associations, which rarely occurred; long calls (whoops) were given exclusively by males, and food long calls at fruiting trees appeared to discourage rather than encourage other subgroups to join the caller(s) (van Roosmalen 1985). In contrast, on Barro Colorado Island in Panama, males of *A. geoffroyi* are most frequently found in tightly bonded all-male associations rather than with females and immatures (Eisenberg and Kuehn 1976, Milton 1993). There are no systematic field data on long-call initiation by spider monkeys on Barro Colorado Island, but observations suggest that males give most such calls; however, in contrast to the situation in Surinam, other spider monkey subgroups may then join the caller(s). To add complexity, study of another call (whinny) by *A. geoffroyi* in Costa Rica shows that it is given more frequently by females than by males and more frequently by dominant than by subordinate animals and that on hearing such calls other subgroups frequently joined the caller(s) to feed (Chapman and Lefebvre 1990).

Why these behavioral differences exist in spider monkeys is not known. Longer study at each site may show that such differences indicate points on a continuum of potential spider monkey social behavior, reflecting perhaps the particular composition and relationships of individuals in the community at the particular time each study was made or some other factor(s) such as food density and distribution. However, since spider monkeys are not generally regarded as possible analogues for some stage of human evolution, these apparent behavioral differences within and between the sexes in spider monkey species and populations have not been interpreted in the same light as those of chimpanzees and bonobos.

By directing our attention to the need for more data on both ape species and particularly bonobos, Stanford provides a valuable perspective—we do not have to look far into the past to recall how, as more field data emerged, the sunny image of the playful, fruit-eating chimpanzee at Gombe was gradually revealed to have a darker side which included the enthusiastic hunting of animal prey, savage attacks on chimpanzee neighbors, and, at times, cannibalism. Who can say what a longer period of time spent studying wild bonobos will reveal? Perhaps in fact all mammal species, just like us, have both a lighter and a darker side?

Stanford has done a good job both of reviewing the available information and of directing attention to the potential biases and preconceptions we may bring to our research and its interpretation. Future fieldwork should clarify just how different the chimpanzees and bonobos are in their social behavior and provide some explanations for differences observed. Regardless of what is ultimately concluded about these ape species, whether the roots of human behavior stem from ancestors more closely resembling the present-day image of the common chimpanzee or that of the bonobo will likely continue to be fruitlessly debated. However, if forced to choose between the two current popular images of these two apes, after some 25 years spent in anthropology departments I believe I'd have to cast my vote for the common chimpanzee!

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After decades of research at multiple sites, it is perhaps surprising that we do not yet understand chimpanzees and bonobos well enough to tell them apart with confidence. Because of their utility as referential models of human ancestors and the ease with which such models become conflated with those ancestors (Moore 1996), it is especially important to understand what we know and do not know about these apes (see, e.g., Moore 1992). Stanford's paper represents an important cautionary tale. For example, in his figure 1, the closest agreement occurs between points G and K, representing sites that have a primary investigator in common (Richard Wrangham); the next level of clustering appears to place K, G, and L (where most researchers have been European or American) together, with the predominantly Japanese sites M and W separate (L and W represent bonobos). Do methodological and/or definitional differences overwhelm taxonomic and ecological ones? Many factors are involved in our attempts to distinguish and define pongid reality, and, as Stanford suggests, our views of apes are subject to strong biases because, in part, they reflect biases about ourselves.

After that initial surprise, some readers might feel smug about progress in their own fields, but this would represent a serious misunderstanding. The reason we do not "understand chimpanzees" (or bonobos) is the same as the reason that after about 2,000 years of formal inquiry we still cannot say confidently that we "understand humans." As long as we see tribes, cultures, species as categorically unique examples of different essences, we are not likely to get much beyond naming the beasts of the field and the birds of the air.

For example, there is debate over whether Taï chimpanzees are "bisexually bonded," unlike the "male-bonded" community described for Gombe (Boesch 1996, Doran 1997), and a similar though less marked difference has long been noted between Gombe and Mahale (Kawanaka 1984). It also appears that Taï lacks the greater male relatedness observed at Gombe (Gagneux, Boesch, and Woodruff n.d.). As Stanford shows (and both Boesch and Doran note), bonobos can be seen in some sense as exhibiting an extension of the trend among chimpanzees toward larger, more stable parties in less seasonal habitats. This trend obscures the categorical meanings of "male-bonded" and "bisexually bonded"; since average degree of relatedness and average party size/duration can in principle vary continuously across the full possible range, trying to determine the truth value of the assertion "chimpanzees are male-bonded" is like answering yes or no to the question "Are humans monogamous?" Altmann and Altmann (1979) pointed out 20 years ago that such subtly different sociodemographic settings can have profoundly significant behavioral consequences.

Discovering the degree to which taxonomic categories (and, by implication, genes) constrain sociodemographic continua is a central goal of primatology. Only by recognizing the underlying conceptual continuity can the meaning of local perturbations due to phylogeny be understood; only by recognizing the nonphylogenetic forces promoting categorical essentializing can we understand and compensate for them. This paper is a real contribution to this effort.

However, Stanford does not escape essentializing. A minor example: "eventually, female chimpanzees establish themselves as members of a new community" implies that this is universal; it is not (Moore 1993). Sweeping the up to 50% of females who remain in their natal communities (Pusey, Williams, and Goodall 1997) under the archetypal rug can only obscure the reasons most of them emigrate. A more significant example: Stanford points out that our extravagant view of bonobo sexuality is based largely on captive studies and implicitly dismisses these as "not reflect[ing] naturalistic mating patterns." Perhaps not, but if bonobos use sex to "cope" with social stress in ways that chimpanzees do not, then elevated sexuality in captivity for one but not the other is perfectly understandable and provides insight into how these apes work. "Captive artifacts" are only scientifically misleading if one assumes that there is one species essence best revealed in one type of setting.

Finally, Stanford states that "males sometimes offer meat to females and receive matings in the process"; "in the process" is ambiguous but implies temporal proximity and a causal connection. The sources cited do not support this statement. Females in estrus are more successful at begging for meat from males (Teleki 1973), and males are more likely to hunt in the presence of swollen females (Stanford et al. 1994). Males appear to use meat tactically amongst themselves in status politics (Moore 1984*b,* Nishida et al. 1992). Females are more likely to engage in restrictive (i.e., temporarily exclusive) mating with males who, on average, share meat more frequently with females (Tutin 1979). Finally, females who receive meat more frequently tend to have greater reproductive success (McGrew 1992).[1] None of these studies directly address the "process" responsible for the patterns. It would be surprising if chimpanzee meat sharing were not involved in complex feedback processes contributing to long-term male-female relationships, sexual and other (analogous to male-male relationships [Moore 1984*b*]). However, the only attempt to test this notion found no support for it (Hemelrijk, van Laere, and van Hoof 1992). Stanford may be correct, but aside from this one study of captive chimpanzees the problem simply has not yet been formally been examined. As Stanford et al. (1994) point out, there are no data showing that the sharing male receives extra copulations from swollen female recipients as a result of his sharing.

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The most unusual and striking aspects of bonobo society are either ignored or inadequately addressed in Stanford's article, and therefore the argument that bonobos and chimpanzees are behaviorally more similar than they are commonly portrayed is unconvincing. For instance, until intensive study of the bonobo began there was no evidence that either female bonding or female dominance over males occurred routinely within any of the living Hominoidea. Recent captive studies of bonobos, however, reveal that females are remarkably skillful in establishing and maintaining strong affiliative bonds with one another. In grooming, body contact, playing, following each other, and staying in proximity, females preferentially select other female rather than male partners (Parish 1996). Moreover, females control access to highly desirable food, share it with each other more often than with males, engage in same-sex sexual interactions to reduce tension, and form alliances in which they cooperatively attack males and inflict blood-drawing injuries (Parish 1996).

Females preferentially associate with each other in the wild too: 20% of party compositions in Lomako contained only females (average 2.48 females/party [Fruth 1995]). Fruth (1995: vii) asserts that "females show a high degree of association, form coalitions, and dominate the society" (on the basis of 4,400 field hours and 1,200 hours of direct observation in Lomako from 1990 to 1994).

Like their captive counterparts, bonobo females in the wild control highly valued food resources such as duikers (Hohmann and Fruth 1993), displace males (except for sons of dominant females) from key feeding sites, aggressively chase and attack males, and intervene in (and apparently sometimes decide the outcome of) male-male disputes involving their sons. Even the social status of a fully adult male is greatly influenced by his mother's rank. A formerly high-ranking male becomes peripheralized upon his mother's death—thus son's rank is influenced by mother's rank rather than vice versa (Furuichi 1989, Idani 1991, Ihobe 1992). Stanford's suggestion that males defer to females rather than females' dominating males is unparsimonious to say the least: how often has dominance behavior in male chimpanzees been ascribed instead to female deference? The assessment that the bonobo pattern is mere male "deference" or "female feeding priority" is based upon one abstract reporting chasing and fleeing interactions involving unhabituated, unidentified individuals over an unspecified observation period (Wood and White 1996). Yet observations of female aggression coupled with male submission are available for identified habituated individuals from both the Lomako and the Wamba research site (e.g., Fruth, cited in de Waal 1997; Furuichi 1989, 1997; Kano 1987, 1990; references in Ihobe 1992). Although males in the wild are not severely injured by females (perhaps because escape opportunities are enhanced in an unconfined environment), they certainly cower and flee when females act aggressively.

Intergroup interactions (characterized here as aggressive and territorial in both species) in fact illuminate another striking difference between bonobo and chimpanzee social systems. Bonobo intergroup encounters

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[1] McGrew failed to correct for female ages; when this is done, the effect is nonsignificant for survival to 1 year ($U = 6$, $p = 0.222$, two-tailed) but becomes marginally significant for infants surviving to 5 years ($U = 3$, $p = 0.056$). That the effect increases with infant age is intriguing in light of nutritional arguments; given a relationship between female rank and meat access (Boesch 1994), one wonders what might be the relationship among meat access, rank, and female reproductive success (cf. Pusey, Williams, and Goodall 1997).

very rarely involve any contact aggression and instead rely upon vocal exchange (Idani 1990, Ihobe 1992). Even more remarkable, females freely mate with males from other groups in the presence of males from their own communities (e.g., Idani 1990), a nearly unimaginable scenario for chimpanzees.

Territoriality in bonobos is much relaxed relative to that in their congener. More than 66% of the home range of one Wamba community overlaps with those of other groups (Kano and Mulavwa 1984). Bonobo males travel alone more often than would be expected from the socionomic sex ratio (Fruth 1995), which would not be predicted if males were in danger from males in other communities. Chimpanzee males found traveling alone by males from other communities, in contrast, are often killed.

Finally, the most obvious chimpanzee/bonobo difference in sexual behavior is ignored: sexual behavior in bonobos encompasses all possible age and sex combinations (e.g., de Waal 1990). Moreover, sexual interaction is routinely used for nonreproductive goals (tension reduction, bartering for social favors, sex-for-food exchanges).

One major similarity ignored in this review is that females of both species mate with males outside their communities. Bonobo females mate openly during intergroup encounters. Chimpanzee females in at least one community manage to circumvent extensive male mate-guarding strategies to conceive with males outside of their own communities (Gagneux, Woodruff, and Boesch 1997).

We expect similarities in two closely related species within the same genus. Equally, we expect that variation in ecological opportunity and constraint will have led to diverse selective pressures and consequent differences in behavior after speciation. An exclusive focus on similarities does more than obfuscate half of the picture: it is impossible to weight the importance of shared traits without comparison with the species' differences. A comparison/contrast (as well as an examination of causal factors other than a rather postmodernist deconstruction of the researchers) would be more likely to produce a strong contribution to our understanding of the behavioral ecology of the two *Pan* species.

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Bonobos and chimpanzees are clearly closely related and display many behavioral and ecological similarities. The tendency to emphasize their differences is reinforced by the resistance of many to retaining the name of "pygmy chimpanzee" for *Pan paniscus,* on the ground that *Pan troglodytes* must then be called "common." Yet whatever the colloquial name, both are clearly chimpanzees.

Given the behavioral flexibility of both species, combined with the often profound intraspecific differences between study populations, it is difficult to identify species-typical social behaviors that reliably separate the two chimpanzees. In many respects there is a continuum between the two species, often depending on ecological conditions. For example, when female chimpanzees are in large food trees, they groom each other at frequencies comparable to bonobos (Ghiglieri 1986). Male affiliation is more difficult to compare because grooming may reflect tension reduction among competitors (de Waal 1987). Male *P. troglodytes* frequently groom one another, as do male *P. paniscus* at Wamba. Affiliative behavior is considerably less frequent among male *P. paniscus* at Lomako (White 1992), where parties are small and unprovisioned. However, at Wamba parties are considerably larger, to the extent that one community is considered to be in contact for the entire day (Furuichi 1989). At Lomako, large groups with multiple males are rarely observed for extended periods of time, but when they do occur males that are normally intolerant of each other may engage in long and intense grooming bouts. However, these exchanges appear to be tense interactions rather than the relaxed grooming sessions more commonly observed between females. Therefore, males in groups that cannot or do not split may groom one another extensively as a component of competition over access to females. Clearly, the characterization of social bonding is complicated by the multiple functions of affiliative behavior reflected by the occurrence of grooming in both friendly and unfriendly contexts.

Intraspecific variation in *P. paniscus* behavior may also complicate comparisons of reproductive ecology. For example, the reduced fission and fusion in the Wamba study communities may influence calculations of the number of estrous females in parties. When the whole community is together all parties will be scored as containing estrous females even if only one female is in estrus. In contrast, because the communities at Lomako are commonly split into several smaller parties, the percentage of parties containing estrous females is usually low. In the 1984–85 field season, only 22% of parties contained fully tumescent females on the basis of simple counts of the number of parties containing reproductive females in the two study communities (White, unpublished data). This is very different from the figure of 100% cited for Wamba in Stanford's figure 1 and more comparable to the data on *P. troglodytes* at Gombe and Mahale. When all females are present in a group, males will presumably prefer to mate with the most swollen females. In contrast, in small parties lacking a tumescent female, which are more common at Lomako, male mating choices may show more variation.

Differences in methodology also complicate comparisons of mating frequency at the Lomako and Wamba field sites. At Wamba, most observations are not from follows of focal animals (Furuichi 1987). At Lomako, focal-animal sampling is used so that mating frequencies can be calculated for individual females at different

TABLE 1
Frequency of Mating by Females at Lomako

Sexual Swelling Size-Class[a]	Observed Matings While Focal Animal[b]	Expected Frequency of Matings[c]
0	2	2.9
I	5	3.9
II	0	14.7
III	2	4.5
IV	0	0.4
V	7	4.5
VI	21	4.8
VII	0	1.3

SOURCE: White (1986).
NOTE: Observed and expected distributions are significantly different ($G = 35.42$, $p < 0.001$).
[a] Swelling classes increase in size, with class VII being maximally tumescent.
[b] A frequency of zero does not mean that a female was not seen to mate but indicates that she did not mate while she was the focal animal.
[c] Based on the proportion of focal sampling spent on a female with a swelling of that size-class.

stages of their sexual swelling (White 1986: table 1). The results (table 1) show that although females mate at all stages of the cycle, they actually mate less than expected at full tumescence given the number of observations for that size-class. In contrast, they mate frequently during the stage just prior to full tumescence. This suggests that, although there is an important social function to mating, females become choosier about mates when most likely to conceive.

Despite clear continuities between the two chimpanzees, there are also fundamental differences between them. Female *P. troglodytes* are less social, as evidenced by the small and independent core areas of the females. The distribution of females in these separate but overlapping core areas provides a major incentive for male sociality: a male can cooperate with others to cover the range of more females than he could do alone. In contrast, from the limited data we have available, female *P. paniscus* core areas appear to be as large as, if not larger than, those of the males (White and Lanjouw 1992). These large core areas, which females usually share with their regular female associates, clearly remove one of the main advantages of the cooperative male group. Instead, a situation arises in which a single male can potentially monopolize the mating opportunities within a foraging party (White and Burgman 1990).

P. troglodytes males are characterized as using power for sex, whereas female *P. paniscus* use sex for power. In wild, unprovisioned populations of both species males are socially dominant to females, largely because of sexual dimorphism (Wood and White 1996, White and Wood n.d.). However, coalitions of *P. paniscus* females can dominate males in provisioned and captive populations (Vervaecke, Van Elsacker, and Verheyan 1992, Parish 1994, Furuichi 1989). Coalitions at Lomako, while important, are rarer given the greater degree of fission and fusion and the smaller overall party sizes. Female *P. paniscus* exhibit feeding priority without female social dominance, implying that there is some form of male deference during feeding in this species. Males may use deferent behaviors to influence female mate choice during the highly fertile period of maximal tumescence. The seasonal paucity of economically defensible, large food sources in *P. troglodytes* restricts females from having large core areas and forming strong associations with potential female allies, thus limiting the degree of female choice that can be expressed. The commonly cited dichotomy of "sex for power" in female *P. paniscus* versus "power for sex" in male *P. troglodytes* may be oversimplified; instead, female friendships may force *P. paniscus* males to use individual chivalry rather than group power to obtain mating opportunities.

Reply

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I began working on this article on the social behavior of chimpanzees and bonobos in a fit of devil's advocacy. I welcome the diverse views of my colleagues presented here and remind both reader and commentator that I am arguing not that bonobos and chimpanzees are behaviorally indistinguishable but only that reported differences have been inflated in the scientific and public imagination for a variety of both empirical and nonempirical reasons.

It is important to note one very interesting and significant pattern in the commentaries at the outset. With one exception, all the commentators who have studied either bonobos or chimpanzees *in the wild* agree strongly with my central assertion—that reported differences in social behavior between these two apes are less striking than commonly reported. The two commentators who disagree strongly have studied these apes primarily *in captivity*. This partially reflects a difference in perspective that derives from the behaviors one tends to see in conditions of enforced proximity and observability versus the natural state, but it is also a strong statement about research findings and their "reality" that goes beyond the data and into issues of research context. Every field researcher I know would vehemently disagree with de Waal's assertion that "only captive studies control for environmental conditions *and thereby provide conclusive data on interspecific differences* [emphasis mine]; field studies usually concern different species under different ecological conditions.'' In fact, since evolutionary processes have molded the social behavior of chimpanzees and bonobos in response to the ecologies of African forests, de Waal's assertion is wrong by definition. I therefore find it ironic that the captive researchers (de Waal and Parish) are the two who are critical of my (apparently heretical) departure from a purely empirical analysis to ask whether there are contextual biases that influence research interpretations. The answer, drawn directly from the pattern of the responses as well as from their content, appears to be yes. That contextual bias consists of (1) influences on social behavior itself created by the setting in which the research is conducted (i.e., field or captivity) and (2) the intellectual biases and the sorts of questions that the researcher brings to great ape research depending on where the study is to be conducted. I firmly believe that these two contextual biases combine to produce some of the divergent views arising from captive versus field research on chimpanzees and bonobos.

The following are my responses to specific comments, discussed in order of the vehemence of their disagreement with me:

De Waal and Parish both cite data from captive studies of bonobos and chimpanzees showing that copulation rates are markedly higher for bonobos. De Waal chastises me for failing to ask why, if bonobo hypersexuality is an artifact of confinement, it has not led to oversexed chimpanzees as well. This point is well taken, but again it points out how futile it can be to apply captive data to wild animals. Captivity affects different species in different ways. You will not see 20 orangutans living amicably in a mixed-sex group in an Indonesian forest, nor will you find many zoos in which the chimpanzee community includes a dozen or more fully adult males. I acknowledge that chimpanzees and bonobos differ in sexuality, in particular with respect to bonobo sociosexuality such as genital rubbing. The observation remains, however, that in their natural habitats chimpanzee and bonobo copulation rates and sexual swelling durations are extremely similar.

De Waal's other main criticism strikes me as setting up a ''straw ape.'' He claims that both scientists and the public have been slow to accept the true extent of bonobo hypersexuality because of our squeamishness about depictions of ape sex. This is presumably because the photographs thereof are the nonhuman equivalent of pornography. He suggests that North Americans are simply too puritanical to handle the notion of a sex-crazed, sensuous ape. As I write this piece, Americans are spending many of their waking hours discussing the details of presidential sexual behavior in all its forms, and when not doing so they are listening to the media (the same media that are reluctant to portray bonobo sexuality?) describing it. I therefore do not accept the notion that anyone is reluctant to listen to accounts of bonobo sexual behavior, in either scientific or tabloid forums.

Parish argues with my contentions by reviewing the literature on female bonobo sociosexual and dominance behavior, nearly all of which was also reviewed in my article. Unfortunately, all of the key points that she claims I have ignored are in fact discussed there, in some cases at length. She incorrectly states that I do not mention intercommunity mating by bonobos in my article. In fact, I point out that ''both hostile and peaceful intercommunity encounters are seen, and copulation between females and extracommunity males has been reported'' (p. x, citing Kano 1992). I stick to my original point about territoriality. The number of intercommunity territorial encounters that involve injury even in chimpanzee studies is quite low if one excepts the two ''warfares'' of the 1970s in Gombe and Mahale National Parks. The rate of intercommunity encounters in bonobo society that include aggressive chasing is 50%, and we have spent only a tiny fraction of observation hours watching wild bonobos compared with chimpanzees.

Kano and White et al. both offer their own reviews of bonobo socioecology. Kano agrees with my cross-species comparison but points out two issues that I neglected to mention that differ between the two apes—infanticide and prolonged mother-son relationships—and offers the same view as Parish and de Waal that bonobo intercommunity encounter behavior is in striking contrast to that of chimpanzees. I should have discussed infanticide in chimpanzees, but the explanations for those episodes reported so far (mainly from Mahale) have been enigmatic in that in some cases males may be killing their own offspring. Bonobos have not been reported to kill offspring. White et al. make the very important point that there is intraspecific variation among known bonobo populations that we must take into account when comparing the two species of chimpanzee. White et al. point out that the data I present showing that nearly all parties at Wamba have at least one swollen female do not agree with Lomako data. At Lomako, smaller party sizes mean that the percentage of parties containing a swollen female is low (about 22%, very similar to the Gombe data for chimpanzees). They suggest that this interpopulational variation may produce differences in male-female behavior between the two best-known bonobo sites, and I fully agree.

The other commentators—Fruth, Ingmanson, McGrew, Milton, and Moore—are in more or less strong agreement with my main points. In fact, each strengthens my argument about chimpanzee-bonobo differences by adding evidence that I overlooked. McGrew feels that I have not gone far enough in my critique, pointing out that *Pan paniscus* occurs not only in rain forest but in other habitats as well. This suggests that future research in other areas of Congo will yield a wider range of socioecology than has been observed so far. He also points out that the interspecific data on swelling durations as percentages of the menstrual cycle that I present in table 1 may be due only to sampling error based on small *N*'s—in other words, that bonobo swellings may not be extended at all compared with those in chimpanzees, except in the raw number of days that a female is partially tumescent.

Moore argues that currently accepted differences between chimpanzees and bonobos based on field data could be due as much to methodological differences between research teams as to actual differences in the animals. If so, it would not be the first time that divergent data collection techniques produced divergent results in the practice of equally sound science. One criticism by Moore—claiming that my statement that chimpanzees offer meat to females and receive sex in exchange is unsupported—is addressed by my work in press (Stanford 1998) documenting cases at Gombe in which sex and meat do indeed appear to be exchanged directly.

Fruth points out that I missed published literature on bonobo meat eating (Hohmann and Fruth 1996) that would have further strengthened my case. I did speculate that future field study might reveal that bonobos hunt and eat meat far more than has recorded thus far, given that neither Wamba (because of human poaching of potential bonobo prey) nor Lomako (because of lack of habituation) has been an ideal site for observing hunting. Fruth cites further information on bonobos' hunting of duiker antelope. Females usually control the carcass and share only with other females. This is exactly the opposite of the situation in Gombe chimpanzees, in which males make nearly all kills and females who do manage to possess meat virtually never share with other females. This may support my argument that male bonobos are unlikely to hunt if they expect to lose distribution control of the carcass to females. Fruth also correctly reminds us that plant food sharing in bonobos (and also in chimpanzees) is more common and perhaps as important as meat sharing.

Ingmanson agrees with my point that, more than any interpretive bias, the factor that has prevented a more accurate picture of bonobo social life from emerging is heavy reliance on detailed captive data but only preliminary field data. She also corrects me for saying that observations of bonobos at Wamba have been done largely in the artificial feeding area, noting that researchers have followed the animals in the forest as well for the past decade. I stand corrected on this point.

Finally, Milton draws a valuable parallel between our lack of understanding of the social ecologies of these apes and the situation in studies of other primates such as the New World monkeys. In urging more research into the causes of intraspecific variation in grouping patterns, she brings home the central point—the difference between these two fascinating great apes and why their social traits have been misunderstood. The bottom line, contained in my paper and in all the responses to it, is that we need to learn much more about them, particularly about bonobos. This is not just a self-perpetuating academic exercise; long-term field research is the backbone of an effective conservation effort. Bringing more information to light on the ecology, social lives, interpopulational variation, and cultural traditions of our two evolutionary siblings is the best way to ensure that they will have a future on Earth alongside their vastly more abundant human kin.

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