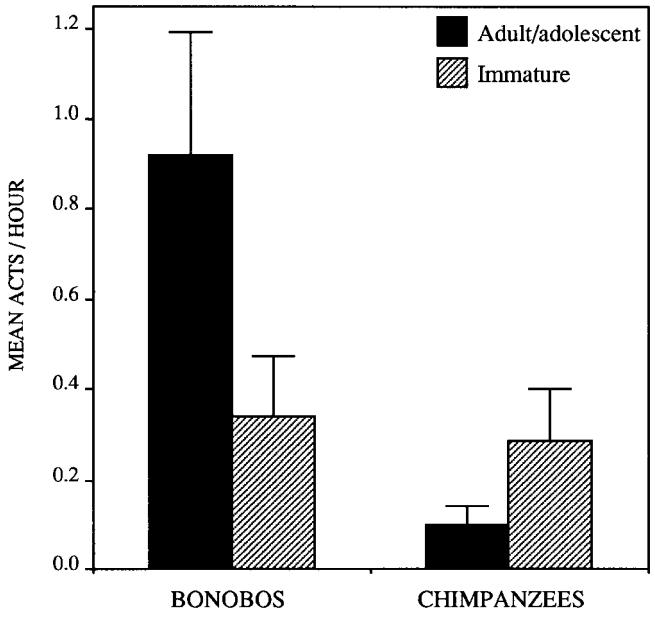

FIG. 1. *Mean (+ SEM) number of sociosexual acts initiated per hour per individual for the San Diego bonobos and an outdoor colony of chimpanzees at the Yerkes Primate Center's field station, separately for adults and adolescents (*black*) and younger individuals* (hatched). *The adult rate was significantly 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