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FOOD SEASONALITY AND SOCIOECOLOGY IN *PAN*: ARE WEST AFRICAN CHIMPANZEES ANOTHER BONOBO?

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ABSTRACT Comparative feeding ecology of African apes has recently been intensively investigated principally for testing the THV (terrestrial herbaceous vegetation) hypothesis. The hypothesis argues that peaceful behavioral nature observed in bonobo (*Pan paniscus*) compared to chimpanzee (*P. troglodytes*) is derived from presence of sufficient THV as fallback foods during lean periods, resulting from habitat segregation from more herbivorous gorillas. There was some supportive evidence for the hypothesis such as presence of feeding competition for fibrous foods between chimpanzees and gorillas in sympatry. However, many cast doubt on the function of THV to maintain female cohesiveness. Overall, the ecological and social causality theorized in the THV hypothesis appears sound, but THV itself unlikely plays a major role, although critical data, bonobo ecology in particular, are still missing. Observed behavioral variation among chimpanzee subspecies suggests that West African chimpanzees are behaviorally more peaceful than East African subspecies. Intensive comparison of some socio-ecological parameters between Bossou and Kibale chimpanzees supported this idea. Data suggested that, also in this case, THV consumption is unlikely a key factor. Because West African chimpanzees, like bonobos, have probably been segregated from gorilla habitat for considerable amount of time in their evolutionary history, collective influence from coexisting with gorillas, not a competition over a single food source, must be responsible for socio-ecological differentiation observed among bonobo, Western chimpanzees, and Eastern chimpanzees.

Key Words: THV; Gorilla; Feeding ecology; Fallback foods; Violence.

INTRODUCTION

Intensive field research on wild chimpanzees (*Pan troglodytes*) since the 1960s has revealed many behavioral characteristics that were thought to exist only in human societies, upsetting our conventional concept of humanity. For example, wild chimpanzees have been observed to commit “inhuman” violence, such as assault and infanticide on group members, and even wage “wars” between communities. Such acts were previously only attributed to humans, the “fallen ape”. Twenty-one episodes of infanticide have been observed among East-African subspecies (Arcadi & Wrangham, 1999), and cannibalism by the killer was also observed in some cases (e.g., Suzuki, 1971). The struggle of males for dominance is often violent, and in one case an alpha male in Gombe, Tanzania, was severely injured as a result of mob violence inflicted by other members of its group (Goodall, 1991). In Gombe, it was also reported that a group attacked the males in a reduced neighboring group, which ultimately dissolved (Goodall, 1986: 503–514); attacks by males from a neighboring group are also presumed to have caused the extinction of a group in Mahale, Tanzania (Nishida *et al.*, 1985).

The bonobo (*Pan paniscus*) is morphologically similar to the chimpanzee, and genetic distances indicate that the two species diverged about two and a half million years ago (e.g., Horai *et al.*, 1992). The first substantial field study of the bonobo was only started in 1973 (see Susman, 1984, for earlier studies). As studies have progressed, it has become clear that bonobo behavior and society are unexpectedly different from those of chimpanzees. In chimpanzee societies, adult males, who are responsible for most of the violence, always dominate females. However, there seems no clear dominance relationship between males and females in bonobo society, and as a result, their conflicts are largely situation-dependent (Kano, 1986). As for inter-community (or unit-group) interactions, although there appears to be some tension between males, females appear relaxed and even exchange social behavior, such as grooming and "G-G rubbing", during group encounters (Kano, 1986). Furthermore, in one case a female of one group mated with a male from another community in front of the males of her own group (Idani, 1990). Moreover, no infanticide has been reported in the bonobo.

What is the key factor that explains the remarkable differences between these two closely related apes? The answer probably lies in the relationships between females. Both the chimpanzee and bonobo have a so called "fission-fusion society", in which the community members form temporal subgroups or parties, with their constituents changing over time (Nishida, 1968; Kuroda, 1979). Despite the overall similarity, there appear to be considerable differences in some essential aspects of the social structures of the two species. In chimpanzee society, males tend to be cohesive and sociable, whereas females tend to be aloof and asocial (Wrangham & Smuts, 1980). In contrast, bonobo females are observed to be relatively cohesive and social (Kuroda, 1980). Bonobo females sometimes cooperatively defend themselves from attacks by males (Kano, 1986: 238), while this is rarely observed for chimpanzees in Gombe or Mahale. It seems reasonable to suppose that female gregariousness and sociability maintain the "peaceful" nature of bonobo society. If this is true, then why do female bonobos act in such a manner?

THE THV HYPOTHESIS

An ecological explanation for the difference in female cohesiveness between chimpanzees and bonobos is the so-called "THV hypothesis" (Wrangham, 1986). In a previous paper, Wrangham demonstrated that chimpanzee females disperse to minimize feeding competition between individuals (Wrangham, 1980). In line with this argument, he argues that bonobo females must face less feeding competition than chimpanzee females for ecological reasons.

Both the bonobo and chimpanzee depend on ripe fruit as their staple food,

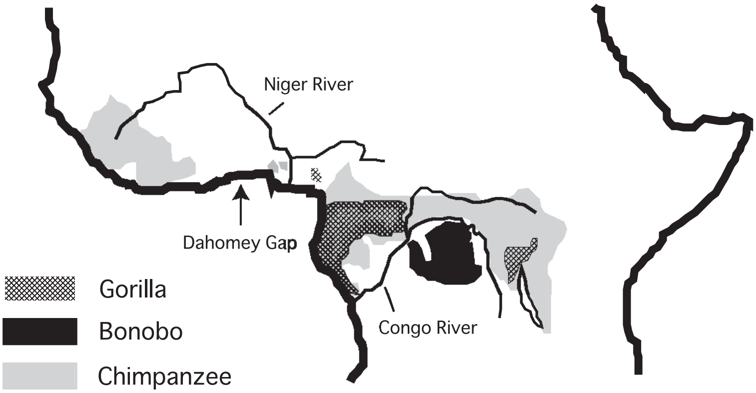

Fig. 1. Habitat of African Apes.

but also feed on foods such as leaves, herbs, bark, insects, and so on (Nishida & Uehara, 1983; Idani *et al.*, 1994). Ripe fruit is of high nutritional quality, but is only available seasonally, because most trees synchronize their fruiting time under the influence of biotic and abiotic factors (van Schaik *et al.*, 1993). Thus, feeding competition between frugivores is expected to increase during seasons of fruit scarcity. In fact, a significant correlation between fruit availability and party size was observed in the chimpanzees of Kibale Forest, in Uganda, suggesting that females disperse to decrease feeding competition when fruit is scarce (Wrangham *et al.*, 1992).

Why can bonobos maintain larger parties? Since the early field studies, the pith of terrestrial herbaceous vegetation (THV) has been described as an important food category in bonobos (Badrian & Malenky, 1984; Kano, 1986). Compared to ripe fruit, THV is uniformly distributed in the habitat and available year round. If the consumption of THV is sufficient for bonobos (but not for chimpanzees) to compensate for the lack of fruit during periods of fruit scarcity, bonobos may be able to maintain larger parties.

There is an interesting difference in the geographical distribution of chimpanzee and bonobo habitats. Bonobos live exclusively on the left bank of the Congo River, where there are no gorillas, while chimpanzees live only on the right bank, where they are sympatric with gorillas (Fig. 1). Compared to chimpanzees, the diet of gorillas is composed of much more fibrous foods, such as leaves and THV. Mountain gorillas are an extreme example, and as much as 85% of their total dietary intake consists of leaves and THV pith (Fossey & Harcourt, 1977). Thus, chimpanzees may have to compete with sympatric gorillas for THV pith, whereas bonobos may be able to eat THV freely without competition. This difference is presumed to be the ultimate cause of chimpanzee-bonobo differences (Wrangham, 1986).

EVALUATING THE THV HYPOTHESIS

Ecological studies of African apes have progressed remarkably since the late 1980s. Most of these studies were intended, either explicitly or implicitly, to test whether the THV hypothesis explains chimp/bonobo differences.

The data come from three sets of studies: 1) bonobo studies, 2) chimpanzee studies conducted at sites where gorillas are sympatric, and 3) chimpanzee studies from sites without gorillas. The ideal comparison should be made between 1) and 2), because this assesses the direct influence of the existence of gorillas and it may best represent the past situation when the bonobo and chimpanzee actually diverged. Unfortunately, observations are often difficult in the second category, since direct observations of chimpanzees are rarely possible. Therefore, category 3 studies are important because they provide supplementary and indicative information replacing the data for category 2, and they may still represent the hard-wired nature of chimpanzees after their divergence from bonobos. Below, I summarize the results from several different perspectives.

I. Feeding Competition for THV between Gorillas and Chimpanzees

An essential element of the THV hypothesis is whether there is feeding competition for THV between sympatric gorillas and chimpanzees. Long-term ecological studies in the area where gorillas and chimpanzees coexist clearly show that the diets of both species largely overlap (Lopé, Gabon: Tutin & Fernandez, 1993; Ndoki, Congo: Kuroda *et al.*, 1996; Kahuzi-Biega, D.R. Congo: Yamagiwa *et al.*, 1996), and the percentage overlap is greater for fruit (Tutin & Fernandez, 1993). Fruit occupies a large portion of the diets of both frugivorous chimpanzees and western and eastern lowland gorillas, which share the same habitat with chimpanzees (e.g., Sabater Pi, 1977, Yamagiwa *et al.*, 1996).

In the case of THV consumption, gorillas persistently eat much more THV than chimpanzees (Tutin *et al.,* 1991; Kuroda *et al.*, 1996). Moreover, although fecal analysis has revealed that THV consumption increases during periods of fruit scarcity in both species (Kuroda *et al.*, 1996; Tutin *et al.*, 1997), the increase is greater in gorillas, while chimpanzees appear to depend persistently on fruit (Tutin *et al.*, 1991). These results imply that some degree of scramble competition for THV may exist between gorillas and chimpanzees, and the amount of THV available for chimpanzees may be reduced by competition with gorillas.

II. Feeding Frequency for THV in Bonobos and Chimpanzees

Another key element of the THV hypothesis is whether bonobos consume more THV than chimpanzees living with gorillas do. Therefore, it is important to determine the actual THV intake of the two species. In Wamba and Lomako, in the D.R. Congo, bonobos spend about 2% of their total feeding time feeding on THV (White, 1992). On the other hand, there are no reliable data from direct behavioral observations of chimpanzees in sympatry with gorillas. Currently, it is impossible to compare the time spent feeding on THV between the two species where conditions are influenced by the existence or absence of gorillas.

For chimpanzees outside present gorilla habitat, the time spent feeding on THV was 12% (Chapman *et al.*, 1995) to 17% (Wrangham *et al.*, 1996) in Kibale, 3.2% in Budongo, Uganda (Newton-Fisher, 1999), 8.8–16.9% in Mahale (Matsumoto-Oda, 2002), 5% in Bossou, Guinea (Yamakoshi, 1998), and 3% in Taï Forest, Côte d'Ivoire (Boesch, 1996). Compared with the bonobo data mentioned earlier, it cannot be concluded that bonobos eat more THV than chimpanzees do. However, possible observational biases must be considered, because THV feeding mostly occurs on the ground, where direct observations are difficult in less habituated communities, such as at Lomako. Therefore, the lower percentage of time spent feeding on THV in bonobos might be an underestimation.

Fecal analysis might be a better way to compare the dietary profiles of chimpanzees and bonobos, because it is free from the above-mentioned observational bias. The percentage fibrous content of feces measured by wet weight was higher in Lomako bonobos than in Kibale chimpanzees (10.90%, n=81 and 2.79%, n=73 respectively, Malenky & Wrangham, 1994). This may be positive evidence that bonobos eat more THV than chimpanzees, but again the chimpanzee data were from a site with no gorillas.

Fecal analysis was also compared between properly selected sites for Lomako bonobos, Ndoki gorillas and chimpanzees, and Kibale chimpanzees, although the parameter used was the proportion of feces containing fibrous matter, which is a cruder estimate than wet weight (Malenky *et al.*, 1994). The prediction from the THV hypothesis is that the Ndoki chimpanzees, which are sympatric with gorillas, should have a smaller proportion than the Ndoki gorillas, Kibale chimpanzees, and Lomako bonobos. In fact, the proportion of feces with fiber was 40% (n=42) for Ndoki chimpanzees, 62% (n=29) for Ndoki gorillas, 94% (n=839) for Kibale chimpanzees, and 68% (n=81) for Lomako bonobos.

III. Fruit Scarcity and THV Consumption

The THV hypothesis assumes that THV is a good alternative source of nutrition that is sufficient to support higher group cohesion when ripe fruit is unavailable. Therefore, it is important not only to observe the total THV consumption, but also its seasonal relationships with fruit availability and party size. At Lopé, Ndoki and Kahuzi-Biega, sites of gorilla/chimpanzee cohabitation, the fibrous content of chimpanzee feces was greater during the non-fruiting season (Tutin *et al.*, 1991; Kuroda *et al.*, 1996; Basabose, 2002). However, no data are available on the seasonality of party size, due to the difficulty in observing the chimpanzees directly.

For Lomako bonobos, fruit availability and party size showed a significant positive correlation. However, when sex differences were considered, only the number of males in the party contributed to the tendency, and there was no relationship between fruit availability and the number of females in the party (White, 1999). This suggests that bonobo females maintain higher cohesion, even in the fruit-scarcity season. On the other hand, the frequency of THV consumption, measured using either the amount of THV fiber in feces (Malenky & Wrangham, 1994) or the observed feeding time (White, 1999), was not correlated with fruit availability. Bonobos consumed THV at a relatively constant rate (White, 1999). Since the total time spent feeding on THV was not substantial at Lomako, as stated above, it seems unlikely that THV utilization enables the stable female cohesion seen in bonobos.

As for the chimpanzees living in sites without gorillas, the fibrous content of chimpanzee feces increased during periods of fruit scarcity at Kibale (Wrangham *et al.*, 1991), suggesting that THV supplemented ripe fruit. However, the party sizes of Kibale chimpanzees decreased markedly during periods of fruit scarcity (Wrangham *et al.*, 1992). This suggests that although much THV is eaten in Kibale, it does not effectively buffer the fruit shortage. At Bossou, party sizes were relatively stable and there was no apparent relationship with fruit availability, which fluctuated widely seasonally (Fig. 2). THV was consumed

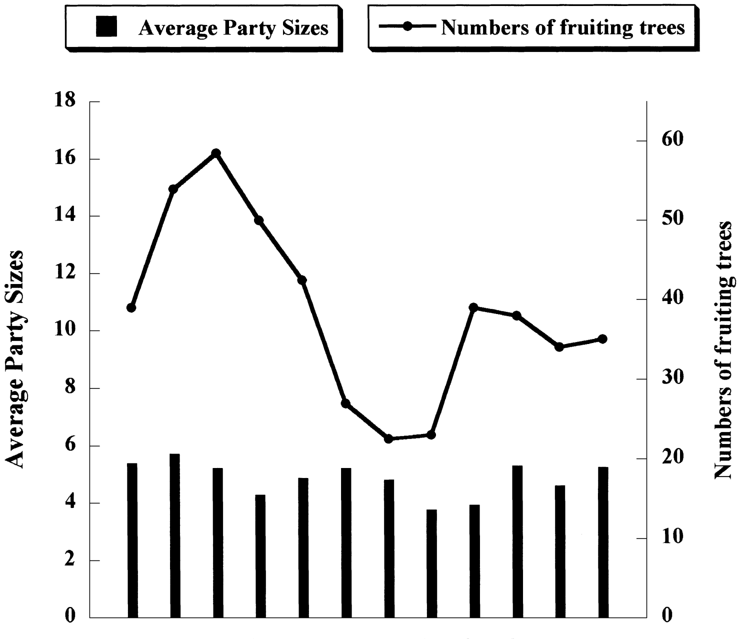

Fig. 2. Party Size and Fruit Availability at Bossou.

A party size is defined as the number of individuals seen together geographically. A new count was made when any change in party composition was observed. Dependent youngsters (0–7 years old) were not regarded as party members. Data were collected in 1995. See Yamakoshi (1998) for further details on the sampling methods. The total number of observed parties was 1,226 (monthly average: 102±27, n=12). The average party size during this 12-month period was 4.95 (n=1,226). The data on fruit availability were taken from Yamakoshi (1998).

evenly throughout the year and there was no sign of a complementary relationship between time spent feeding on THV and time spent feeding on ripe fruit (Yamakoshi, 1998). Also in Kalinzu Forest, Uganda, THV consumption did not increase during low-fruit season (Furuichi *et al.*, 2001).

IV. THV Density and Nutrition

The THV hypothesis assumes that bonobos eat more THV than chimpanzees because more THV is available in bonobo habitat than in chimpanzee habitat, where THV availability is limited by the presence of gorillas. Investigations have compared THV available to the two species in terms of density and nutritional content.

A comparative study of THV density examined bonobo habitat in Lomako, chimpanzee habitat in Kibale, and chimpanzee-gorilla habitat in Ndoki (Malenky *et al.*, 1994). THV was significantly more abundant in Lomako than in Kibale, but the differences were not significant between Lomako and Ndoki or between Kibale and Ndoki. However, ecological parameters such as climate, altitude, and vegetation differ markedly between Kibale and Lomako, and neither habitat contains gorillas, so that the results do not seem to make much sense for the THV hypothesis.

Nutrition analysis demonstrated large differences in the nutritional profiles of THV among research sites. The THV in Lomako contained much protein, but was low in calories. In contrast, the THV in Kibale was characterized as having a lower protein/higher calorie content (Malenky & Wrangham, 1994). Since most ripe fruit is a good source of calories, but not protein, it is considered that the Kibale THV is nutritionally appropriate as an alternative to ripe fruit, while the Lomako THV is not (Malenky & Wrangham, 1994). This prediction nicely fits the above-mentioned behavioral observation that seasonal THV consumption in Kibale increased with decreasing fruit availability, but THV in Lomako was consumed constantly, independent of the change in fruit availability. This suggests that THV in Lomako is not consumed as a fruit substitute, but to meet constant nutritional requirements (possibly for protein), contrary to the prediction of the THV hypothesis.

V. Summary of the Evidence

The above results can be summarized as follows: 1) chimpanzees in sympatry with gorillas appear to have a limited competitive relationship for THV; 2) preliminary fecal analyses suggested that bonobos eat more THV than chimpanzees, while the results of direct observation were ambiguous; 3) chimpanzees' THV consumption increased when fruit was in short supply, but its effect on maintaining party size was unclear, while bonobos seemed to eat THV regardless of season and the numbers of females in parties were relatively constant, even in during periods of fruit scarcity; and 4) there seems to be a difference in THV density between sites, but its effect on ape feeding behavior is unknown; there were marked differences in the nutritional content of THV, which had a higher protein and lower caloric content in bonobo habitat.

Evidence supporting the competitive relationship between gorillas and chimpanzees over THV as a food resource came mainly from fecal samples, in which it is difficult to discriminate THV fiber from other food fibers. A recent preliminary survey conducted at Petit Loango, Gabon, found that the densities of both gorillas and chimpanzees were higher there, although the habitat contains only a small amount of THV (Yamagiwa *et al.*, 1995). This suggests that THV may not be a crucial food for chimpanzees and/or gorillas, although further confirmatory observations are needed. It is possible that gorillas and chimpanzees do not compete exclusively for THV, but compete for particular fibrous foods or for all fibrous foods when fruit is scarce.

Bonobo feeding ecology seemed contrary to the prediction of the THV hypothesis in some important domains. No clear correlation was found between bonobo female cohesiveness, fruit availability, and THV feeding rate, as seen above. Wrangham himself admitted the failure of the THV hypothesis to explain this negative evidence, and proposed a modified hypothesis (Wrangham *et al.*, 1996). According to the revised hypothesis, THV is divided into high and low quality THV (H-THV and L-THV, respectively), based on the distinction made by Kuroda *et al.* (1996), and H-THV replaces the THV of the original hypothesis. H-THV is rich in protein and is actually a much preferred food type for Ndoki gorillas (Kuroda *et al.*, 1996).

The revised hypothesis seems to have a serious problem in reasoning and practicality. The original hypothesis focused on fruit scarcity as the main reason for party size decrease, and on THV as a fallback food to replace fruit. Since fruit is the main food of chimpanzees and bonobos, and is a good source of energy, but not of protein, the caloric content of THV is important. Since the revised hypothesis postulates that H-THV contains high quality protein, it is not logical to link calorie shortage and protein intake. An investigation of seasonal changes in protein availability is certainly a good focus for future studies.

Overall, it is probably too early to determine the validity of the THV hypothesis, because critical data are still missing. There are almost no direct observations of chimpanzees cohabiting with gorillas. Moreover, the systematic ecological data for bonobos come mostly from a single study site, Lomako. Although the areas in question are currently politically unstable, more ecological data are desperately needed for as many populations of these apes as possible.

OBSERVED VARIATION IN CHIMPANZEE SOCIOECOLOGY

I started my review by mentioning the intriguing difference in the sociability of female chimpanzees and bonobos. As I have shown, it is not yet possible to confirm a causal flow of interrelated ecological variables, such that reduced feeding competition over reliable foods during critical periods makes bonobo females more gregarious and less vulnerable to male harassment, while decreasing offensive male behavior, such as infanticide, as anticipated by the THV hypothesis.

Interestingly, there have been claims that in some populations of the western subspecies of chimpanzee (*Pan troglodytes verus*), females are not as asocial as in the eastern subspecies (*P. t. schweinfurthii*). The frequency of proximity and grooming between western females was higher than the expected value for Bossou chimpanzees (Sugiyama, 1988). Similarly, female chimpanzees at Taï were reported as associating closely with each other, and forming "friendships" (Boesch, 1991). Those authors suggested that the between-female social relationship appears more similar to that of bonobos (or even to female-bonded macaques) than to the East African chimpanzee subspecies.

There is also no clear evidence of infanticide by males in any western subspecies population. A single case of an infant's death with subsequent cannibalism was reported from Taï as a likely case of infanticide, although the killing was not observed and the consumers of the meat were females (Boesch & Boesch-Achermann, 2000: 33–34).

These observations imply a systematic difference in female sociability and "violent" behavior between the two chimpanzee subspecies, aligning the West African chimpanzee subspecies with bonobos behaviorally (Table 1). Can these differences be explained by the ecological logic of the THV hypothesis?

I. Kibale-Bossou Comparison

Since not much THV was consumed at either site, as discussed above, the

Table 1. Comparison of the Basic Ecological and Social Variables among Chimpanzee and Bonobo Study Sites

Site	Degree of fruit seasonality	Frequency of THV feeding	Existence of other fallback foods	Degree of party size reduction*[1]	Frequency of female-female grooming	Presence of infanticide
Bonobo						
Lomako	Low?	Low	?	Small	High	No
Wamba	?	?	?	Small	High	No
Chimpanzee						
Taï	High	Low	No?	?	High	No?
Bossou	High	Low	Yes	Small	High	No
Kibale	High	High	No	Large	Low	Yes
Budongo*[2]	Low	Low	?	Small	?	Yes
Gombe	?	Low?	?	Large	Low	Yes
Mahale	?	?	?	Large	Low	Yes

*[1] During seasons of fruit scarcity. See text for references.

*[2] The ecological setting in Budongo seems similar to those of bonobo sites, but the social variables there are likely consistent with the East-African pattern. It will be important to elucidate whether the seemingly aseasonal fruit availability in Budongo is typical or temporal on a long-term basis.

THV hypothesis in its original form seems unlikely to explain the suggested behavioral differences between East and West African chimpanzees. However, the variables listed in Table 1, other than THV feeding, seem consistent with the idea that the mitigation of food scarcity by a particular type of food may lead females of the West African subspecies to be more gregarious than those of the eastern subspecies.

The clearest contrast in the possible effects of fruit scarcity on the ecological variables for females is found between Kibale and Bossou (Table 1). There is a season with severe fruit scarcity at both sites (Wrangham *et al.*, 1992; Yamakoshi, 1998). Kibale chimpanzees do not seem to have good fallback foods other than THV, and their party sizes are markedly reduced when fruit is in short supply (Wrangham *et al.*, 1992). On the contrary, Bossou chimpanzees can rely heavily on two non-fruit fallback foods, palm pith and nuts, which are abundant throughout the year, and can be accessed with the aid of tools to compensate for the fruit scarcity (Yamakoshi, 1998). However, party size does not differ much between seasons (Fig. 2). Such a tool tradition is obviously absent at Kibale (Whiten *et al.*, 1999; Yamakoshi, 2001).

The social interactions between females are quite different at these two sites. Female chimpanzees at Kibale spend only a tiny amount of time grooming each other. Surprisingly, Wrangham *et al.* (1992) did not observe any female-female grooming during intensive focal following in an 11-month study. On the other hand, a 12-month study using nearly the same sampling method revealed that Bossou females spend a substantial time at female-female grooming (Table 2; Fig. 3).

It is still speculation whether the higher female cohesiveness and sociality in Bossou have any effect in reducing male aggression. Quantitative data on aggressive behaviors are still lacking for Bossou chimpanzees, but my qualita-

Table 2. Distribution of Grooming Time among Age-sex Classes at Bossou

Focal animals	% time spent grooming*[1]	Grooming Partner*[2]						
		Adult female	Subadult female	Adult male	Subadult male	Offspring	Immature	No. focal individuals
Adult females	9.8±5.5	1.8±1.5	0.4±0.7	3.3±1.6	0.3±0.3	4.1±2.0	0.0±0.0	7
Subadult females	3.6	0.6	—	0.0	0.9	—	0.0	1
Adult males	11.8	2.8	0.5	—	2.5	—	0.0	1
Subadult males	5.1±2.2	0.4±0.1	0.9±0.9	3.4±3.7	1.3±0.4	—	0.0±0.0	3
No. of partners		7	1	1	3	6	6	

The original data were sampled by focal animal sampling with 10-minute units ("TMS study" *sensu* Wrangham *et al.*, 1992. See Yamakoshi, 1998 for details).

*[1] Average proportion of the time in the activity budget spent engaged in grooming interaction by individuals in each age/sex class.

*[2] Values are the average proportion of grooming time relative to the time observed together in the same party on a dyad basis.

Adult: 12 or more years old. Subadult: 8–11 years old. Immature: 0–7 years old.

The sampling method and parameters are virtually identical to those of Wrangham *et al.* (1992).

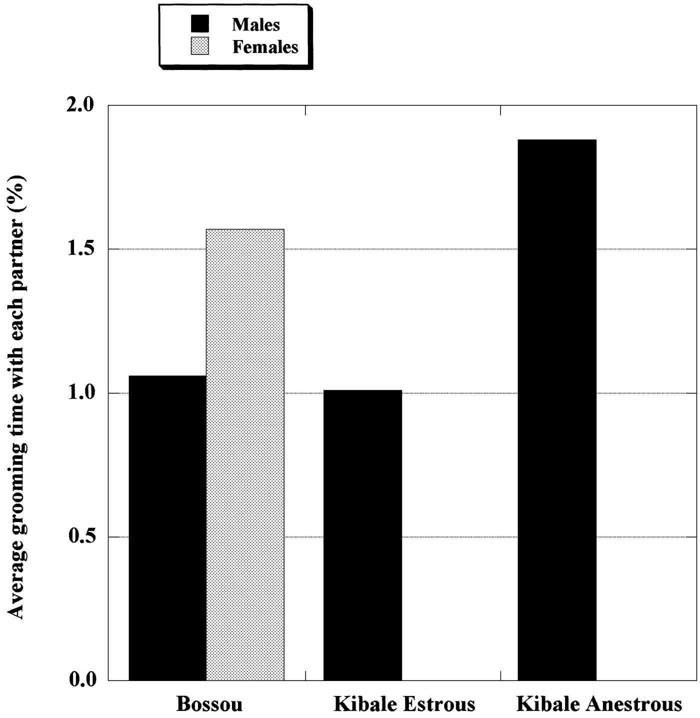

Fig. 3. Grooming Partners for Females at Bossou and Kibale.
The data are from Table 2 of this study and Table 3 of Wrangham *et al.* (1992), which employed the identical sampling method. Only the samples in which females were focal animals were used in the analysis. Adults and subadults of each sex are clumped because of the small sample size for the Bossou community (only one adult male and one subadult female). Number of partners: Bossou males (n=4); Bossou females (n=7); Kibale males (n=13); Kibale females (n=12).

tive impression is that aggression can begin with a small incident between individuals, and often ends with a fuss involving many adult members. A display by an alpha male is the most common cause of such aggressive interactions, but in such cases, the attacked female screams and these screams result in intervention by other females. Occasionally, a female can chase away an alpha male, when backed by the screams of other individuals. Most of the Bossou chimpanzees bear evidence of injury and the majority of these injuries appear to be on the face, mostly the ears. I have directly observed fights that caused such injuries, but these involved alpha males attacking juveniles. I have not seen any serious fights between adults so far. These impressions suggest that it is quite likely that Bossou females can effectively counter male aggression and this may prevent infanticide in this community.

However, there are explanations for female cohesiveness and sociality in Bossou other than a lack of fruit scarcity. Perhaps the small semi-isolated habitat of Bossou allows females less room to escape, similar to the situation of captive chimpanzees in enclosures (de Waal, 1994). Moreover, a recent hypothesis on sex difference in travel distances predicts that if a habitat is small enough to allow females to follow fast-moving males, the community could retain larger average party sizes (e.g. Wrangham, 2000). The habitat of Bossou chimpanzees is relatively small, and it is surrounded by large areas of human activity, such as farmland, fallow bush, and grassland. However, chimpanzees frequently visit these surrounding areas to look for farm crops without facing serious danger, thanks to the inhabitants' traditional reluctance to harm the chimpanzees (Sugiyama, 1978; Yamakoshi, 2002). So, the situation is hardly similar to those of captives. In fact, Bossou males have a much longer average daily travel distance than the females (Takemoto, 2002).

It is also possible that because there is no community directly adjacent to the Bossou community, the rate of genetic interchange could be lower and relatedness among females could be higher. So, the high between-female grooming of Bossou chimpanzees could be explained by the fact that they are simply grooming their relatives. However, a preliminary genetic analysis comparing the mitochondrial DNA D-loop between Bossou and the nearest community, Nimba, demonstrated that the Bossou community is not very isolated from surrounding communities genetically (Shimada *et al.*, 2001). Thus, it seems plausible that the cohesiveness and sociability of Bossou females is due to the presence of effective fallback foods.

II. Are West African Chimpanzees Another Bonobo?

The comparison of ecological and social variables between Kibale and Bossou using a nearly identical sampling method appears to support a causality similar to that of the THV hypothesis, although THV itself does not play a role (Table 1). This suggests that the main premise of the THV hypothesis is socio-ecologically sound, and is also applicable to the differences between the western and eastern subspecies. The question, then, is why the feeding competition among females during food scarcity is supposed to be stronger in East African chimpanzees than in Western subspecies, as well as Bonobos.

One of the central elements of the THV hypothesis is the geographical segregation of bonobo habitat from that of gorillas. Of note, the western subspecies of chimpanzee is also currently allopatric with gorillas (Fig. 1). Little is known about the geographical distribution of gorillas, chimpanzees, and their ancestral forms in African prehistory, and there is no reliable information on the existence of gorillas in West Africa beyond the Dahomey Gap.

The western subspecies is estimated to have separated from the other subspecies about 1.6 million years ago, which is not much different from the estimated time of divergence between chimpanzees and bonobos of 2.5 million years ago (Morin *et al.*, 1994). During this time, the African climate has fluctuated extensively, with the driest and coolest periods being 2.4 and 0.9 million years ago (Vrba *et al.*, 1989). The African rain forest must have shrunk and recovered accordingly.

Similar to the situation hypothesized for bonobo habitat on the left bank of the Congo River, there are no mountains higher than 1800 m in the West African chimpanzee habitat west of the Dahomey Gap. Therefore, this was likely an unsuitable habitat for gorillas during drier periods, and the Western subspecies of chimpanzees must have evolved and survived in a habitat where there were no gorillas for a considerable length of time, perhaps for, at least, one million years. Therefore, if the THV hypothesis is correct in suggesting the importance of the absence of feeding competition (although not necessarily for THV) between gorillas and bonobos, it could also be applied to the western subspecies of chimpanzee.

Intriguingly, there appears to be a systematic difference in female sociality between *Pan* populations that live (or have lived) with gorillas (the central and eastern subspecies of chimpanzees) and without gorillas (bonobos and the western subspecies of chimpanzees). What aspect of feeding competition is significant in this evolutionary scenario? Although the original THV hypothesis stressed competition for THV pith, this has received little empirical support.

One of the impressive findings of recent ecological studies in areas where gorillas and chimpanzees coexist is that the feeding profiles of the two species are broadly similar. Unlike folivorous mountain gorillas (Fossey & Harcourt, 1977), lowland gorillas eat much more fruit, and the difference between their diet and that of chimpanzees seems quantitative rather than qualitative (Tutin & Fernandez, 1993; Kuroda *et al.*, 1996; Yamagiwa *et al.*, 1996). Although previous studies focused mainly on the fibrous food intake (e.g., THV) by the two species, the existence of phylogenetically close species in the same home range must have diverse effects on all aspects of their life. It would be fruitful to compare the behavior of the two African apes, not only in the use of one particular foodstuff, but over a broad range of foraging behaviors, such as the ranging style of one species as a function of the behavior of the other.

Further ecological studies on the three African apes are solely needed to verify and improve “THV” hypothesis. And in revising the hypothesis, it is worth regarding West African chimpanzee subspecies as another important focus.

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