

Female Contributions to the Peaceful Nature of Bonobo Society

TAKESHI FURUICHI

Although chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are closely related, females of the two species show surprisingly large differences in many behavioral aspects. While female chimpanzees tend to range alone or in small parties during non-estrous periods, female bonobos aggregate even more often than do males. Female chimpanzees do not have frequent social interactions with other females, whereas female bonobos maintain close social associations with one another. Although the ranging patterns of chimpanzee parties are generally led by males, female bonobos often take the initiative in ranging behavior. While female chimpanzees usually do not exhibit estrus during postpartum amenorrhea or pregnancy, female bonobos exhibit a prolonged pseudo-estrus during such non-conceptive periods. Studies of these two species have also shown great differences in agonistic behaviors performed by males. Male chimpanzees frequently fight with other males to compete for estrous females, but male bonobos seldom do so. While there are many records of infanticide by male chimpanzees, there is no confirmed record of such an event among bonobos. Several cases of within-group killing among adult male chimpanzees have been reported, but there is no such record for bonobos. While intergroup conflicts among chimpanzees sometimes involve killing members of the other group, intergroup conflicts among bonobos are considerably more moderate. In some cases, bonobos from two different groups may even range together for several days while engaging in various peaceful interactions. I will address two important questions that arise from these comparisons, exploring why females of such closely related species show such clear differences in behavior and whether or not the behavioral characteristics of female bonobos contribute to the peaceful nature of bonobo society.

The social systems of both chimpanzees and bonobos are characterized by fission and fusion. Their

social groups, called unit groups or communities, are semi-closed and have fairly stable membership, except for the transfer of females between unit groups.^{1–4} Within these groups, however, animals characteristically split into smaller subgroups or parties, in which memberships flexibly change over time.^{1,4–9} In this review, I refer to a unit group or community as a group and to a temporary association of group members as a party.

panzees.^{6,10} However, in a recent comparative study using data available from various study sites and groups, I showed that there is considerable within-species variation in party size and that there is no significant difference between the two species.¹¹ On the other hand, this study also confirmed that there is a significant difference between these species in the average number of individuals in a party relative to the total number of individuals belonging to the group. This proportional measure is called the relative party size¹² or the attendance ratio.¹³ Boesch showed that the relative party size was larger for bonobos than for chimpanzees.¹² I showed the same pattern highlighting a significant difference in the two species' attendance ratios (27% to 51% for bonobos versus 9% to 30% for chimpanzees).¹¹

Figure 1 illustrates these differences by comparing group and party sizes between the E1 group of bonobos at Wamba, in the Luo Scientific Reserve, Democratic Republic of the Congo, and the M group of chimpanzees in Kalinzu, Uganda. In both studies, we followed the largest parties that we could observe at the time, using the same 1-hour-party method developed for the comparison of party sizes and compositions across different species and sites.¹⁴ As noted, the total numbers of individuals in 1-hour parties were not significantly different between the two species. However, while almost half of the group members were found in the 1-hour parties of bonobos, a smaller proportion of members were found in those of chimpanzees. In particular, there is a marked between-species difference in

Takeshi Furuichi's research interests include the sexual behaviors, life histories, and ecological adaptations of great apes, with the ultimate goal of understanding the processes involved in hominoid evolution. He conducts long-term field research on bonobos at Wamba in the Luo Scientific Reserve, Democratic Republic of the Congo, and chimpanzees in the Kalinzu Forest Central Reserve, Uganda. E-mail: furuichi@pri.kyoto-u.ac.jp

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GROUPING PATTERNS AND FEMALE INITIATIVE IN DETERMINING RANGING

Early studies on the ecology of bonobos suggested that their party sizes were larger than those of chim-

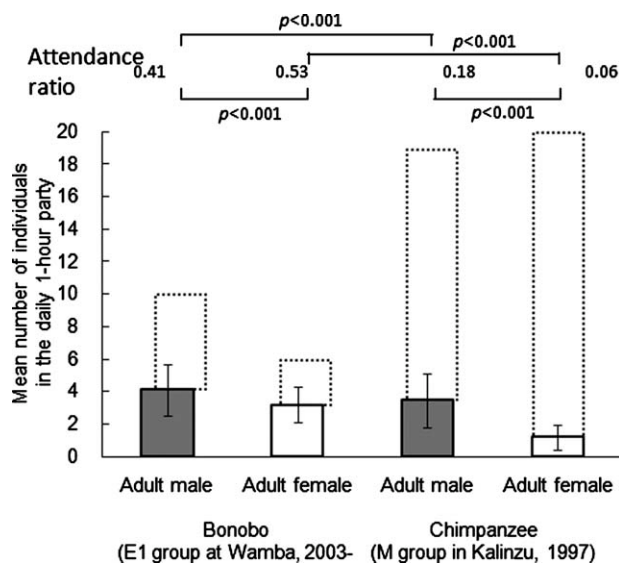


Figure 1. Comparisons of party size and composition in the M group of chimpanzees in Kalinzu and the E1 group of bonobos at Wamba. We recorded individuals observed in each 1-hour period while following a party, which approximates the number of individuals ranging and feeding together. The length of bars with solid lines represents the average number of individuals found in the 1-hour party; the length of bars with dotted lines represents the number of all individuals belonging to the unit-group. See Hashimoto, Furuichi, and Tashino¹⁴ and Mulavwa and colleagues⁹¹ for more details.

female attendance ratio, with less than one-tenth of the female chimpanzees, but almost two-thirds of the female bonobos, found in parties.

Although the term “fission-fusion” is usually used to describe the grouping patterns of both chimpanzees and bonobos, the species differ substantially in their cohesiveness. As seen in an example from Mahale, Tanzania,¹⁵ fission and fusion of parties occurs frequently among chimpanzees. Because different parties may range in distant areas, only rarely can a researcher observe all members of the group within the same day.¹⁶ In Kalinzu, where we have studied chimpanzees since 1992, several years elapsed between observations of certain females that usually ranged in the periphery of the home range. Most likely these females were not observed during pregnancy or lactation periods because they were primarily ranging with their dependent infants and juveniles, apart from other members of the group (Hashimoto and Furuichi, unpublished data).

In contrast, most members of the bonobo group at Wamba can be observed daily. Before 1996, when

our study was interrupted by political instability, we occasionally provisioned the bonobos, either at sleeping sites or at a permanent provisioning site. During this period, we observed an average of 88.9% of adult or adolescent females and 87.6% of adult or adolescent males.⁹ Since 2003, in studies of the same group under completely natural conditions, all group members were present on many observation days, especially during the high-fruited season. For example, during the 12 months of 2008, all of the adult group members were observed on 35 of the 124 days on which parties of the study group were observed from sleeping site to sleeping site. Eighty-three percent (S.D. = 27%, median = 100%) of adult females, and 79% (S.D. = 26%, median = 28%) of adult males were observed during each of the 124 days (Sakamaki and co-workers, unpublished data). Although bonobos split into several parties during the day, group members range in adjacent areas and travel in a similar direction, exchanging vocalizations, so that many of them appeared at least once a day in the party we were following.

Various hypotheses have been offered to explain the tendency of female chimpanzees to range alone or in small parties.^{17–21} For example, in a food patch females may be subject to larger costs from contest competition than are males due to their lower dominance status. Foraging in a larger party may increase the frequency of shifts between food patches and thus impose larger costs from scramble competition on females because their lower velocity leads to longer travel times between, and late arrival to, food patches and feeding sites. If these hypotheses are true, then females may avoid large parties in favor of small ones, as was shown for chimpanzees in Kibale, Uganda.¹⁹ This prediction, however, was not verified in bonobos, among which the attendance ratio of females was always higher than that of males, irrespective of party size (Fig. 2). This suggests that the relationship between social grouping and food supply may differ for bonobos and chimpanzees. For example, bonobos often forage on the abundant terrestrial herbs, fruits, and young leaves of small but widely distributed trees as they travel between large fruit trees; this may lower the traveling speeds of parties and thus reduce the costs that females incur by attending large parties. Alternatively, female bonobos may want to attend large parties for social reasons, regardless of the increased feeding costs they may incur. As I will discuss later, females may be able to increase their social status relative to males by aggregating with other females or they may want to range with their sons to support their attempts to acquire higher dominance rank or reproductive success.

Although it is not yet supported by quantitative data, female bonobos appear to be able to determine ranging activity, which seems in part responsible for the cohesive grouping. At Wamba, party movements typically occur when members descend from a tall fruit tree and take a short break on lower trees, observing one another. Some of the males climb down and perform branch-dragging behavior while running on the ground, seemingly to propose a

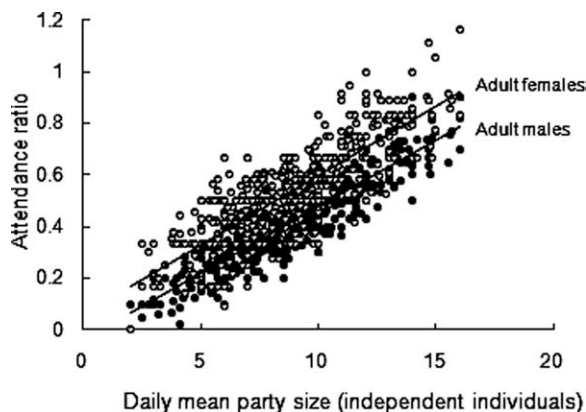


Figure 2. Attendance ratios of males and females of the E1 group of bonobos at Wamba. Each dot shows the daily mean attendance ratio, which is the mean probability with which each male or female was observed in a 1-hour party. The x axis is the daily mean 1-hour party size. The attendance ratio of females exceeded 1 on three days because one unknown female temporarily joined the party of the study group. See Mulavwa and colleagues⁹¹ for details.

direction of movement. However, the entire party does not move until the dominant females climb down and initiate movement in a direction of their own choice. Even when males go off alone to explore distant areas of their home range, they usually return by the evening and rejoin the females if the latter did not follow them (Furuichi, personal observation). By directing a party's movement patterns, females can determine the ranging rate, length of each leg, and day range. This makes it easier for females to attend large mixed-sex parties because they may be able to reduce the feeding costs that result from their lower velocities.

Several other behaviors typical of both male and female bonobos also appear to enhance the cohesive grouping observed in this species although, again, these behaviors have yet to be quantitatively examined. In some cases, when traveling long distances between different areas in their home range, bonobos split into two or more parties, one going ahead and the others remaining behind. In such cases, the parties frequently exchange vocalizations, and some bonobos in the lead party will sit on the ground and look back, awaiting the arrival of those left behind (Furuichi, personal observation). I rarely observed such "waiting" behavior among chimpanzees in Kalinzu. Similarly, when bonobos arrive at a big fruiting tree, rather than climbing up immediately, they

instead wait for other group members to arrive. When the others do arrive, they produce a chorus of soft vocalizations and climb up the tree together (Sakamaki, personal communication). Chimpanzees in Kalinzu sometimes give loud calls to attract other group members to feeding trees, but they never wait for other members to arrive before climbing them.

The two species also exhibit different behavioral tendencies at nightfall. When bonobos prepare to stop for the night, parties traveling separately but in the same vicinity start calling to one another. We call these vocalizations "sunset calls."⁶ In Kalinzu, I rarely hear such calls in the evening among chimpanzees. Bonobo parties sometimes approach one another, exchanging sunset calls, and begin to make nests after they join. This happens most frequently during the high-fruited season. Bonobos usually forage in large parties during the day and aggregate to form even larger parties in the evening; the next morning, they again split into several parties to forage.²² In Kalinzu, there is no tendency for chimpanzees to sleep in parties larger than those formed during the daytime. In Budongo, Uganda, party size tends to drop decisively in the evening before nest-building time.²³ Taken together, such behaviors seem to show that bonobos are highly motivated to range together to the extent that circumstances permit, and that females play an influential role in the maintenance of group cohesion.

CLOSE SOCIAL ASSOCIATIONS AMONG FEMALES

Female bonobos do not merely aggregate, but form close social associations with one another. This is another important difference between female bonobos and female chimpanzees, which do not frequently have affiliative relationships.²⁴

Bonobos form male-philopatric groups.^{10,25,26} Throughout our studies at Wamba, immigration of males occurred only during or following a single period of war in D. R. Congo between 1996 and 2002, when neighboring groups of the main study group, E1, disappeared. Presumably, the remnants of those groups were integrated into the study group.²⁷ Otherwise, there have been no cases of immigration by males.²⁷⁻²⁹ Hohmann and Fruth³⁰ also reported a case of immigration by adult males into the study group in Lomako, but these are the only such cases reported from any of the sites where bonobos have been observed frequently enough to permit individual identification (Wamba, Lomako, and Lui Kotale in D.R. Congo).

As for females, all of those confirmed to be born in the study group at Wamba disappeared by the age of 10 years. If we exclude those that died before reaching 2 years of age, the others all disappeared between the ages of 6 and 10 years. These females were assumed to have emigrated, rather than to have died, because their health conditions were normal before their disappearance. On the other hand, all females from other groups that joined the study group did so at estimated ages of between 6 or 7 and 14 years. Interestingly, all females below the age of 10 years that immigrated into the study group disappeared after a few days to several months. In contrast, most females that immigrated into the study group at estimated ages of 10 years or older eventually had offspring and settled into the group permanently. It seems that young adolescent females who have left their natal groups move from group to group before settling into a final group.²⁷⁻²⁹

While most female bonobos that immigrate into new groups during

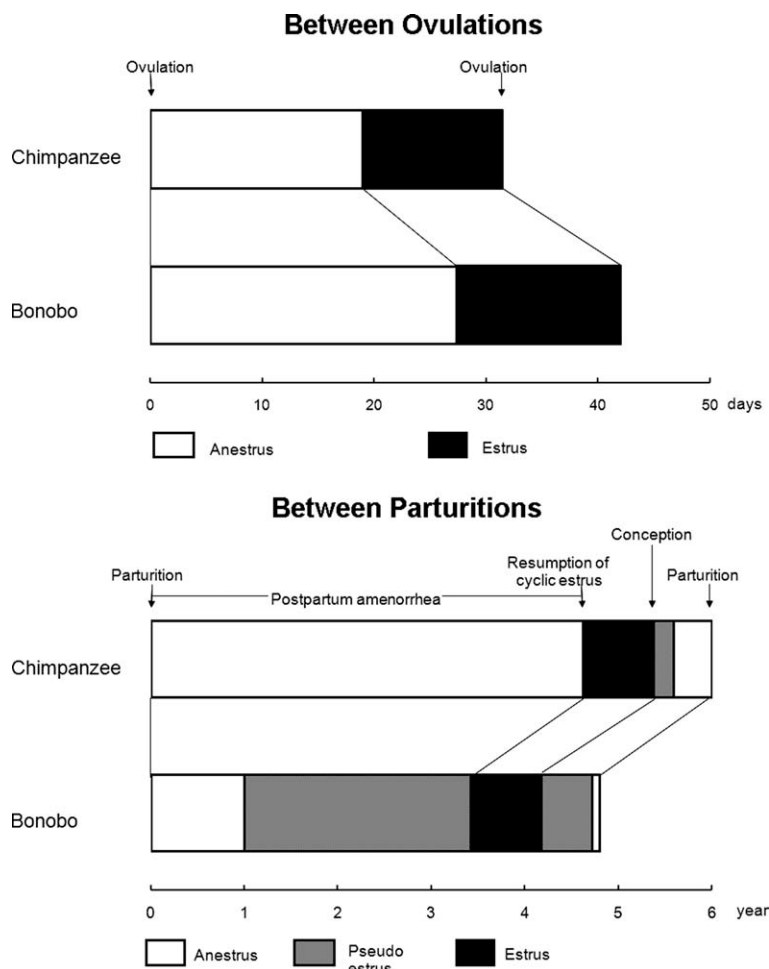


Figure 3. Estrus periods among chimpanzees and bonobos. Because there is no information on the timing with which bonobos resume fertile estrus, I assumed that they have the same interval between resumption of fertile estrus and conception as do chimpanzees.

adolescence experience estrus and copulate with males, several years typically will elapse before they give birth at approximately 13 to 15 years of age.³¹ These females tend to have frequent social interactions with other females that immigrated during the same period or with senior females already established in the group, particularly “specific senior females” who are old and high in rank.^{32,33} Immigrant females are selective in their choice of specific females to associate with, following them as if following their mothers and frequently soliciting them to engage in species-typical “genito-genital rubbing” behavior.¹⁰ They also direct “peering” behavior³² toward these senior females when they are feeding and even beg for food from their mouths. This behavior does not

seem to be aimed at getting food because it occurs even when food is available elsewhere. The real intent appears to be the social interaction gained with these senior females. Through these various interactions, immigrant females establish social bonds with senior females and bonobo females on the whole form tight associations. Although many are unrelated, their tight associations seem to improve their status in a male-philopatric group.

PROLONGED PSEUDO-ESTRUS

Another conspicuous characteristic of female bonobos is their prolonged pseudo-estrus periods.^{9,10,34–37} Like females of many mammals, adult female chimpanzees, except those during adolescent sterility, usually

exhibit limited periods of sexual receptivity during the peri-ovulatory phase of the ovarian cycle, which I call the “estrus period”.^{36,38} A female in estrus has a fully tumescent sexual swelling; periods of sexual attractivity and proceptivity, as well as receptivity, generally coincide with maximal tumescence of the sexual skin.³⁹ On the other hand, adult female bonobos perform similar sexual behaviors and show maximal tumescence even during nonconceptive periods, which I call “pseudo-estrus”. Chimpanzees do not exhibit estrus during their long postpartum amenorrhea, which here represents the period between parturition and resumption of cyclic estrus. However, bonobos resume cyclic estrus much earlier, although the time between parturition and next conception does not differ much between the two species.³⁷ Also, although chimpanzees cease to exhibit estrus within a few cycles postconception, bonobos continue to exhibit estrus until the late stages of pregnancy. Although the physiological mechanism for this pseudo-estrus is not yet understood, it certainly contributes to a female’s coexistence in the group and to the control of male aggression.

Figure 3 diagrams these differences in the estrus periods between chimpanzees and bonobos using data mainly from Mahale and Wamba, with supplementary data from animals in captivity. Female chimpanzees experience estrus for 12.5 days before ovulation in a cycle of 31.5 days.⁴⁰ Although female bonobos sometimes show continuous estrus throughout the menstrual cycle, they also typically show estrus for 14.6 days in a cycle of 42 days.⁹ Thus, the proportion of days spent in estrus during a menstrual cycle does not substantially differ between the two species. On the other hand, there are significant differences in estrus periods during an interbirth interval. Female chimpanzees do not show estrus during postpartum amenorrhea and resume cyclic estrus at 55.5 months after parturition, conceiving 8.9 months thereafter.⁴¹ Visible signs of estrus cease 2.6 months postconception⁴² during the 7.6 months of

TABLE 1. Estrus Sex Ratio of Chimpanzees and Bonobos

	Chimpanzee (Mahale)	Chimpanzee (Gombe)	Bonobo (Wamba)
Proportion of a cycling period during an interbirth interval ^a	0.16	0.11	0.77
Proportion of days in estrus during a menstrual cycle ^b	0.40	0.38	0.35
Proportion of days in estrus during an interbirth interval (a*b) ^c	0.064	0.042	0.27
Adult sex ratio (#adult males/#adult females) ^d	0.27	0.51	0.75
Estrus sex ratio (# adult males/# adult females showing estrus) (d/c)	4.2	12.3	2.8

pregnancy.⁴³ Therefore, female chimpanzees are in estrus for only 12.5 days per cycle over the course of 11.5 months during an interbirth interval of 6 years.⁴¹ In contrast, female bonobos resume estrus 1 year after parturition.¹⁰ Although no information about the timing at which female bonobos resume fertile estrus, judging from the timing of subsequent conception they apparently remain infertile during this period. Therefore, this is a pseudo-estrus without possibility of conception. Female bonobos also show pseudo-estrus during pregnancy until about 1 month before parturition.¹⁰ Thus, the total time that female bonobos show estrus during an interbirth interval of 57.6 months²⁸ is much longer than that for female chimpanzees.

This difference in female receptivity between species may have important implications with regard to the intensity of sexual competition within groups. To test this hypothesis, I compared the estrus sex ratio (or operational sex ratio) between the two species. The estrus sex ratio is defined as the ratio of the number of adult males to the number of adult females showing estrus at a given time. We estimated the estrus sex ratio for chimpanzees in Mahale and Gombe, and for bonobos at Wamba, using published reproductive data^{7,9,10,28,37,40–45} (Table 1; see Furuichi and Hashimoto³⁷ for more details).

The proportions of cycling periods that occur during interbirth intervals are 0.16 and 0.11 for Mahale and Gombe chimpanzees, respectively; for Wamba bonobos, this figure is

0.77, or about 5 to 7 times larger. If we multiply these figures by the proportion of days on which females are in estrus during each menstrual cycle (0.4 and 0.38, respectively for Mahale and Gombe chimpanzees, 0.35 for Wamba bonobos), the proportions of days in estrus during interbirth intervals becomes 0.064 for Mahale chimpanzees and 0.042 for Gombe chimpanzees, while the proportion for Wamba bonobos is 0.27 days. This means that female chimpanzees show estrus on only about 5% of the days in their adult lives, or that, on average, only 1 out of 20 females shows estrus at any given time. In contrast, female bonobos show estrus for as much as 27% of their adult lives, so that at any given time 1 of every 4 females is in estrus. In reality, however, the actual difference is somewhat moderated by the lower adult sex ratio in chimpanzee groups. Although this itself may be a result of the severe intermale competition and resultant killing of infant or adult males, the ratios of the numbers of adult male chimpanzees to that of adult females at Mahale and Gombe were as low as 0.27 and 0.51, respectively, during the study periods. If we take this adult sex ratio into account, the estimated estrus sex ratio becomes 4.2 for Mahale chimpanzees and 12.3 for Gombe chimpanzees. On the other hand, Wamba bonobos have the highest ratio of adult males to adult females (0.75), but the estrus sex ratio is still estimated to be as low as 2.8. Therefore, even for the Mahale chimpanzees, where the number of adult males is less, the estrus sex ratio is still higher than that among Wamba

bonobos. In Gombe, where there are closer numbers of males and females, the estrus sex ratio is much higher than that of Wamba bonobos.

Although it ignores substantial between-group and temporal variation, Figure 4 illustrates the general differences in the sexual relations of chimpanzees and bonobos, using the number of adult chimpanzees in Mahale M group in 1984⁴¹ and the number of adult bonobos and the number of estrous adult females in the Wamba E1 group in 1987–88.³⁷ If we use the estimated proportion of days in estrus, only 2.2 of 35 female chimpanzees, on average, are expected to show estrus at a given time, while 10 adult males compete for access to these females (Fig. 4, top). Although the proportions vary for different groups and study sites, chimpanzee mating behaviors include possessive mating by high-ranking males, opportunistic and promiscuous mating, and mating during consortships.^{1,23,36,40,46–53} In many groups, the alpha males and/or males allied with them may have priority in mating access, so that females cannot usually refuse their copulation attempts. During opportunistic mating, females are sometimes severely attacked by males that attempt copulations.⁵¹ Thus, copulations are, to a large extent, influenced by power games among males, with female choice of mating partners being limited.

Among bonobos, in contrast, although there were only 9 females in the group, a greater number of females (3.1 on average) showed estrus at any given time (Fig. 4, bottom).³⁷ In such situations, it is difficult for an alpha male to monopolize all estrous females. Therefore other males may be able to approach estrous females and solicit them for copulation more freely than can male chimpanzees.^{10,54,55} Copulations are not frequently disturbed by other males at Wamba, although intermale aggression is known to be more frequently observed in the mating context at Lomako⁵⁶ and Lui Kotale.⁵⁷ Under such circumstances, the most important thing for males is not to dominate other males, but rather to be preferred by females as

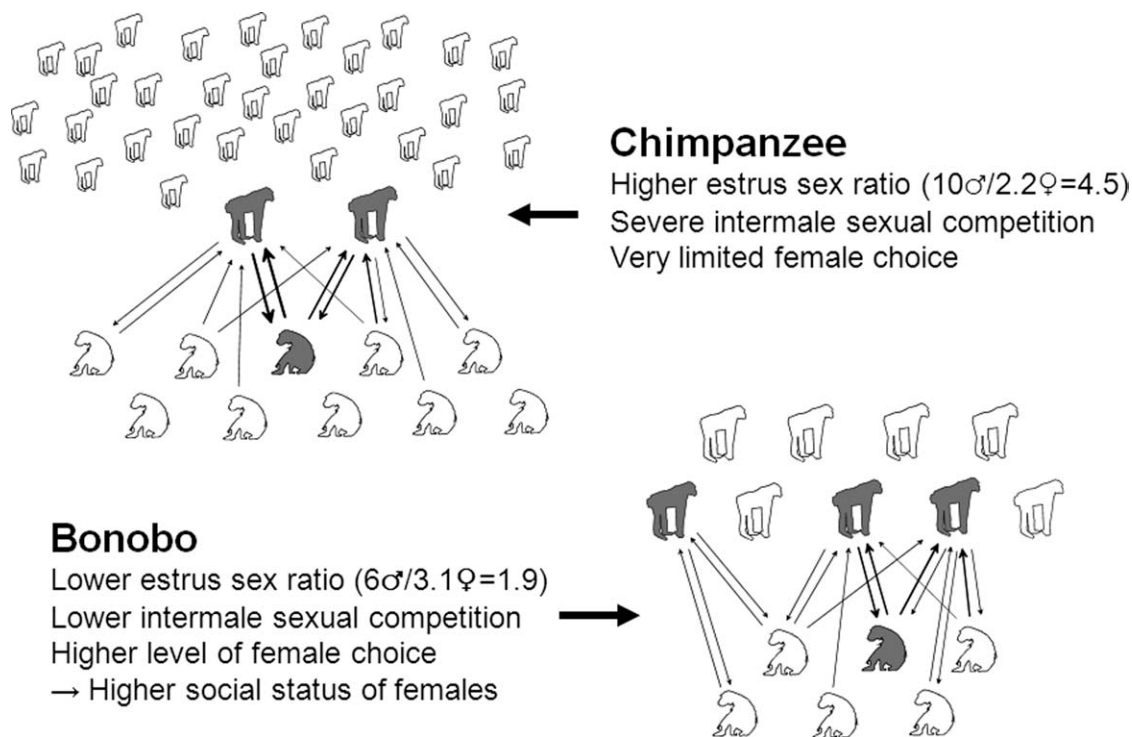


Figure 4. Sexual relations among chimpanzees and bonobos. Females are drawn in upper parts, males in lower parts. Dark colors show estrous females and alpha males. Arrows show the solicitation or acceptance of copulations.

copulation partners. This may be why males rarely attack or attempt to sexually coerce females. Females can easily ignore solicitations by alpha males, and the occurrence of copulation largely depends on whether females accept a male's solicitation.^{10,54–56,58} Thus, with prolonged estrus, females can reduce both excessive sexual competition among and harassment by males.

HIGH SOCIAL STATUS OF FEMALES

If females aggregate in the central part of a mixed-sex party, form close social associations, and are active in mate choice, one naturally assumes that they have high social status. This assumption is true, but the question of whether their social status is equal to that of males, or whether they are actually dominant over males, remains. This has been a controversial topic for quite some time.

In the wild, dominance between males and females is equal or equivocal, but females seem to be dominant

over males where feeding is concerned. Unfortunately, we have only a few reports on the frequency of agonistic interactions between males and females in wild bonobo populations. In a study that I did on the E1 group over a 7-month period (528 hr and 56 min over 97 days), males were dominant over females in 27 cases, while females were dominant over males in 25 agonistic interactions, showing that males and females had relatively equal status.⁵⁸ Most of the male-dominant cases involved display behaviors in which males ran around emitting excited vocalizations, dragging branches, and dashing toward females. Females fled from these males, but such behaviors rarely involved physical attacks. On the other hand, most of the female-dominant interactions represented retreats by males following approaches by females. Some of the cases occurred in feeding situations. For example, when females approached males who were feeding in a preferred position at a feeding site, males yielded their positions to late-arriving females. Furthermore, males usually waited at the pe-

riphery of the feeding site until females finished eating. When overt conflict occurred at feeding sites, allied females sometimes chased males, but males never formed aggressive alliances against females. It is interesting to note that even the alpha male might retreat when approached by middle- or low-ranking females. At Lomako, males were dominant over females in all 11 cases of dyadic agonistic interactions between adults and subadults for which dominance between the participants was decided. However, females had priority of access to food in terms of the order in which individuals entered food patches.⁵⁹ Another study at Lomako showed that the frequency of female aggression against males was more than double that of male aggression against females, opposite to the study at the same site mentioned earlier.⁵⁶

On the other hand, many reports show that female bonobos are dominant over males in captivity.^{60–63} In a comparative study of various captive populations, Stevens and colleagues⁶⁴ showed that the linearity and steepness of dominance vary among captive pop-

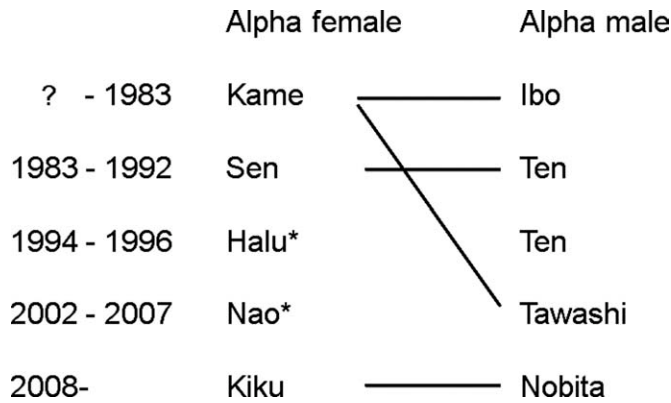


Figure 5. Alpha females and alpha males in each study period. Lines show the mother-son relationships. Asterisks show that those females did not have adult or adolescent sons during the periods of their alpha-female status.

ulations, and that female dominance is not exclusive, which means that not all females are dominant over all males. However, they also showed that the highest ranking individuals were females and the lowest-ranking individuals were males in all of the populations studied. Thus, there really does appear to be a difference in this respect between the social tendencies of wild and captive bonobos.

As noted earlier, females can express dominance in situations involving competition for food. Even when feeding on hunted animals, which are a rare and valuable food resource, females in many cases maintained possession of the kill,⁶⁵⁻⁶⁸ although among chimpanzees males typically monopolize such resources.⁶⁹⁻⁷¹ Therefore, the higher status of females in captivity might be explained by the fact that competition over food occurs more frequently in captivity. However, this will need to be tested through further study of wild populations.

INFLUENCE OF MOTHERS ON THE SOCIAL STATUS OF ADULT MALES

Interestingly, female bonobos aggregate, maintain close social associations, and control social relationships in the group, but they usually do not behave politically or forge tactical alliances in the manner of male chimpanzees. However, there is one important exception to this generalization: given the chance to raise the status of their adult or adolescent

sons, mothers can behave quite aggressively, as we observed in the changes of the alpha female and the alpha male in 1983-84 (Fig. 5).^{58,72}

By 1983, when I started my study, the oldest female, KAME, was the alpha female; her oldest son, IBO, was the alpha male. KAME had two other younger sons, and they always kept close associations. However, TEN, an adolescent son of the second-ranking female, SEN, approached the age of adulthood and began displaying at KAME's three sons. IBO did not show submissive behaviors and, at the end of many such interactions, instead mounted TEN. However, he sometimes left the area to avoid the persistent provocations of the younger TEN.

When males are involved in agonistic interactions, mothers sometimes join to support their sons. However, KAME, who was both pregnant and aged, rarely intervened. In contrast, SEN sometimes attacked KAME's sons to support TEN. On one occasion, IBO fled from SEN after an intense physical fight. A fight between the two mothers occurred five days later, with SEN being the victor. After this, fights between these females occurred several times, but KAME never defeated SEN. Five days later, TEN approached IBO, emitting display vocalizations, as was usual at the time. At first IBO stood bipedally to fight TEN, but then turned his back to present his rump instead, at which point the two males performed rump-rump contact.⁷³ From that time on, SEN and

TEN behaved as the alpha female and the alpha male. Agonistic interactions between these two families became infrequent (Fig. 6).

It seemed that this entire series of incidents was triggered by the challenge of TEN, but he could take the alpha position only when his mother overtook the mother of the previous alpha male and became alpha female. Indeed, SEN was very supportive of her sons. After TEN took the alpha-male position, she persistently supported her 7-year-old second-youngest son. He sometimes behaved dominantly over adults in the group, and SEN threatened them when they resisted.

When we resumed our study in 1994, after a 2-year break caused by political unrest, SEN had died and the second-ranking female, HALU, had become the alpha female. Because HALU's eldest son had died a few years earlier, she had no adult or adolescent son. Thus, TEN continued to be the alpha male. However, HALU was apparently dominant over TEN, so that the highest ranking individual in the E1 group during this period was a female.

Our research was again interrupted by a civil war in 1996. When we resumed our study in 2002, HALU was not in the group, and was presumed to be dead. Although NAO had become the alpha female, she also had no adult or adolescent son to become alpha male. Instead, TAWASHI, the third son of the deceased ex-alpha female, KAME, was in the alpha male position.

In the 2008 study period, we found that KIKU, who had been the second-ranking female, was the alpha female, though we do not know when the rank reversal occurred. During this period, a young adult male, NOBITA, became the alpha male. When we resumed our study in 2002, we had tentatively given all adolescent males new names because it was difficult to confirm the identity of immature males after a 6-year break. However, DNA analyses confirmed that NOBITA was identical to KIKUO, the first son born to KIKU.²⁷ Therefore, it appears that another mother-son pair became the alpha female and male.

Thus, throughout our study of E1 group, which began in 1976, 5 prime or old adult females took the alpha-female



Figure 6. An ex-alpha female, KAME (left), is groomed by the ex-alpha male, IBO (center), and other offspring. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

position. Three of these had adult or adolescent sons at the time, and those males took the alpha-male position. When the other two females without adult or adolescent sons took the alpha position, other males maintained the alpha position, but the alpha female was apparently dominant over the alpha male in one of these cases. Stated differently, 3 of 4 males that have occupied the alpha position at the time of their rank acquisition.

It is clear that females do not reach the alpha female position owing to the high status of their sons because males never support their mothers in agonistic interactions among females. Rather, females support their sons in agonistic interactions among males. Among chimpanzees, males with strong male allies tend to achieve high rank, with males at a prime adult age usually taking the alpha position.^{7,23,47,74,75} In contrast, male bonobos in E1 group tend to obtain the alpha position during late adolescence or early adulthood (estimated ages in years: IBO = <20, TEN = 13, TAWASHI = 22–28, NOBITA = 20). This may have occurred because, except the case of TAWASHI, whose mother had al-

ready died, their mothers were at a prime age at the time of their ascent to alpha male status. In contrast, many prime adult males occupied lower ranks among adult males in both the E1 and E2 groups of bonobos at Wamba, although there were some exception (TAWASHI was the alpha male in the E1 group and KUMA was the alpha male in the E2 group for certain periods). This tendency may be partly explained by the fact that the mothers of those prime adult males had already died.^{58,72}

We may ask, then, why some female bonobos intentionally support their maturing sons' bid for alpha status, despite the fact that they do not often fight with one another or behave politically. I hypothesized that females may compete to increase their number of grand-offspring through the support of their sons.⁵⁸ Although females cannot increase the number of offspring they themselves produce by fighting with other females, they may be able, by raising the social status of their sons, to increase the number of their sons' offspring. Gerloff and colleagues²⁶ reported that at Lomako two males that attained the highest paternity success were sons of high-ranking females. Surbeck⁵⁷ reported that females at Lui

Kotale frequently intervened in the mating attempts of unrelated males or provided their sons with agonistic support when unrelated males tried to interfere with their sons' mating activities. As a result, middle- or low-ranking males had increased mating success when their mothers were present in the party. This kind of support by mothers seems to be a common feature among wild bonobos.

FEMALE ROLE IN PEACEFUL ENCOUNTERS BETWEEN GROUPS

It is well known that intergroup encounters among chimpanzees are aggressive.⁷⁶ At Mahale, during conflicts between groups, males of the K group disappeared one by one, seemingly killed by males of the M group, which finally took over both the home range and the females of the extinct K group.⁷⁷ A similar incident occurred between Kasakela and Kamaha groups at Gombe.^{7,78} After splitting into the two groups, the larger Kasakela group killed the males of the Kahama group, which finally became extinct. During this process, several fatal attacks were observed. Males of the Kahama group sometimes patrolled boundary areas, attacking and killing Kahama males that were ranging alone.⁷ Male patrolling behavior and fatal agonistic interactions have also been observed at Kibale^{79–82} and Kalinzu⁸³ in Uganda, and at Taï in Côte d'Ivoire.⁸⁴

Intergroup encounters among bonobos are also stressful. When they hear vocalizations of other groups, bonobos usually climb up trees and carefully look in the direction of the sounds. They sometimes quietly change their direction to avoid other groups. In most cases, however, they respond to such vocalizations with a chorus of loud calls. The two groups gradually approach each other, exchanging vocalizations. When they finally meet, males often display, but do not usually fight. Although males do not usually merge at the front lines, after a time females do move beyond the front lines and begin to interact with females of the other group, engaging in genito-genital rubbing or grooming. It seems as if they have found old associates or relatives

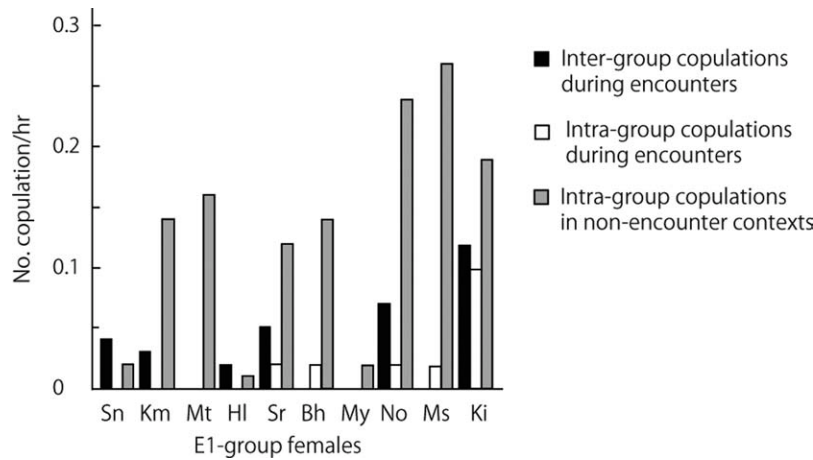


Figure 7. Characteristic features of female bonobos and relationships among them.

in the other group. After the initial excitement has passed, the groups often start feeding in the same tree. Although males tend to stay away from the front lines, it becomes difficult to identify the boundary between the two groups.^{10,85}

In the 1986–87 study period, Idani observed 25 encounters between P group and the main study group, E1, over 3 months.⁸⁵ In all encounters, both groups remained together for long periods. During such encounters, copulations frequently occurred between males and females of the different groups. Figure 7 shows the frequency of copulation by adult females of the study group. E1 females copulated with males of P group with considerable frequency, though less frequently than with males of the same group. Considering only those encounters, E1 females copulated with P males more frequently than they did with E1 males, suggesting that females are eager to copulate with males of different groups. As noted, females move beyond the front lines without hesitation, but males tend to stay within the range of their own group. Therefore, males cannot do anything to restrict females even if they copulate with males of the other group. On the other hand, males can copulate with females from the other group that come into their range without any disturbances from the males of that other group.

Encounters between two groups of bonobos can be intermittently repeated for several days.⁸⁵ It seems that such encounters are stressful for males; they occasionally moved away, vocalizing in an apparent attempt to encourage females to terminate the encounter. However, if females did not separate from the other group, males returned to the encounter. Thus, these peaceful intergroup encounters apparently were led by females. Such encounters appear to hold no risk for females and they gain an opportunity to copulate with extra-group males or socially interact with extra-group females that they may have known

before transferring to their current groups.

Bonobos seem to readily establish peaceful relationships with the groups they encounter, though such relationships are not formed for all combinations of the groups. After the study group E split into E1 and E2 in 1983, the two new groups continued to have peaceful encounters. E1 bonobos also had peaceful encounters with another neighboring group, K, but tended to vacate the area when they heard vocalizations of another neighboring group, B. In the 1980s, the E1 group more frequently had peaceful encounters with P group as they extended their range into the south after splitting off from the original group. After we resumed our study in 2003, E1 group extended its range into the east, and came to have peaceful encounters with a newly identified group in 2010. Peaceful encounters have also been reported from Lomako.⁸⁶ Groups at that site did display to one another, and the frequency of agonistic interactions increased during the encounters. However, members of the different groups also copulated with and groomed one another.

CONCLUSION

This comparison of the social structures of chimpanzees and bonobos

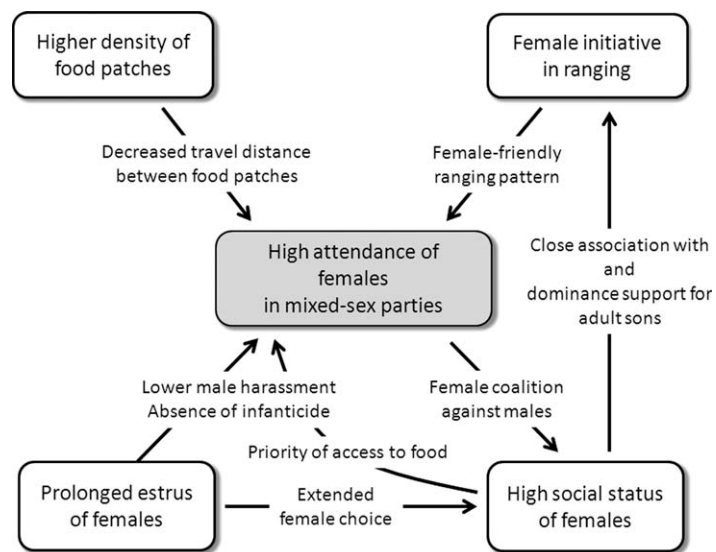


Figure 8. Characteristic features of female bonobos and relationships among them.

illustrates how the nature of societies may change depending on which sex controls behavioral initiatives. Female bonobos are highly gregarious despite living in male-philopatric social groups. They form close social associations and cooperatively defend their high social status against males, severely competing only for the high dominance rank of their sons. The high social status of females and their initiative in social, sexual, and ranging behaviors seem to contribute to the peaceful nature of the bonobo society.

The characteristic features of female bonobos appear to be interrelated and together contribute to the high attendance of females in mixed-sex parties (Fig. 8). First, bonobo habitats, as compared with those of chimpanzees, have higher density of food patches, including large fruit trees and smaller food items on which they forage while traveling between larger trees. Such ecological conditions may decrease the travel distance between food patches,^{11,19,87,88} thus reducing the cost for the slower-moving females. Second, if females can exercise an initiative in ranging, they can avoid incurring larger costs associated with travel than males do, which may promote the aggregation of females in mixed-sex parties. Third, with a prolonged estrus, females mitigate any potential for excessive sexual competition among males and thereby avoid male harassment. In addition, the long periods of pseudo-estrus may prevent infanticide through paternity confusion. The high social status of females may contribute to their aggregation in at least two ways. One way is that females can have priority of access to food and, because of their high rank, avoid both infanticide and harassment by males. Another way is that through their close association with and dominance support for their adult sons, they can take the initiative in ranging. On the other hand, the high degree of aggregation displayed by bonobo females can also contribute to their high social status, through formation of coalitions. The social status of females may also be enhanced by the extended female choice in mating partners resulting from prolonged estrus.

Recent genetic studies have shown that chimpanzees and bonobos diverged within the last million years or so,^{89,90} more recently than was previously thought. It is not surprising, therefore, that chimpanzees and bonobos share many common traits, including physical attributes and their male-philopatric residence patterns. However, something changed for bonobos, probably during a bottleneck period, that altered the sexuality and social status of females. Since chimpanzees, gorillas, and orangutans all share common traits, such as a limited estrus period among females and male dominance, this change seems to be specific to bonobos. Considering the recent divergence of bonobos and chimpanzees, we may infer that small genetic changes occurred in one or a few key features and thus invoked development of the whole social system represented in Figure 8, rather than that the various features evolved independently. For example, if genetic changes occurred in the physiology of females, causing them to show estrus during nonconceptive periods, this whole social system may have developed in an environment with abundant and dense food resources, without requiring many other genetic changes, at least in the early stages. I expect that genetic studies will clarify the small but important genetic differences that can explain the large differences in sexuality and society of the two species in the genus *Pan*.

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