

Demographic Parameters and Life History of Chimpanzees at Bossou, Guinea

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ABSTRACT Demographic parameters of wild chimpanzees at Bossou, Guinea, are presented and compared with those of other populations. The population size of Bossou chimpanzees has been stable over the last 26 years, except during two incidents of partial deforestation. The annual birth rate for a female (mean = 0.194, but 0.165 when the infant survived more than 4 years) and interbirth interval are not much different from those of other study sites. The primiparous age of Bossou chimpanzees, however, is far younger (mean = 10.9 years) than for all other known wild chimpanzee populations. The infant and juvenile survival rate is also the highest (female = 0.64, male = 0.52 for the first 8 years). As a result, the lifetime reproductive success of Bossou chimpanzees is estimated to be highest among long-term study sites. The rate of disappearance from Bossou dramatically increases

during the adolescent stage, and most young chimpanzees disappear before or around maturation. Probably because the environmental capacity for chimpanzees at Bossou is at its limit, many young independent males, as well as females, have to disperse, though others may die. For chimpanzee alpha males of other populations, mature males may be needed as collaborators to defend resources. In the case of Bossou, however, a lack of adjacent groups, conspecific competitors, predators, and perhaps medium-sized mammals as prey for group hunting may eliminate this need of the alpha male for other males. The reasons why all males of other chimpanzee populations persist in being philopatric for life and maintain kin-related male bonds differing from most mammal species, including humans, are discussed. *Am J Phys Anthropol* 124:154–165, 2004. © 2004 Wiley-Liss, Inc.

Demography is an important but basic topic in the ecology of animals because environmental conditions, particularly food abundance, directly influence reproductive success. Food distribution patterns and vegetation type also influence group and individual behaviors such as feeding, ranging, and social behavior. Population density in the habitat, and group size and composition, may affect the life-history strategy of males as well as females. As a result, demography impacts on the life history of individual animals and also the social structure (Altmann and Altmann, 1979). The comparison of these data among populations from different environments is therefore essential for finding out the behavioral and social adaptation as well as phylogenetic constraints of animals.

Although there are many studies on wild chimpanzees (*Pan troglodytes*), since 1960 most of them have focused on social and cultural behaviors, social relationships among group members, and group organization (Goodall, 1986; Nishida, 1990; Boesch and Boesch-Achermann, 1999). Much attention has been paid to the relations between these behaviors and the sophisticated intelligence of apes (McGrew, 1992; Whiten et al., 1999). Far less attention has been paid to the demography of chimpanzees and their adaptation to the environment.

The main reason for this gap must surely be the extremely slow reproduction and long life history of chimpanzees. For example, lactation lasts more than 3 years after birth, and the interbirth interval is said to be nearly 6 years. These intervals are longer than those of humans, and other demographic parameters are near to those of humans. Another reason for a lack of intensive demographic studies on chimpanzees must relate to female dispersal around maturation. This makes it difficult to decide the exact age of adult females and their offspring, as well as the number of offspring borne by a female.

Furthermore, a long-term study confines each researcher to a particular site, so most data are re-

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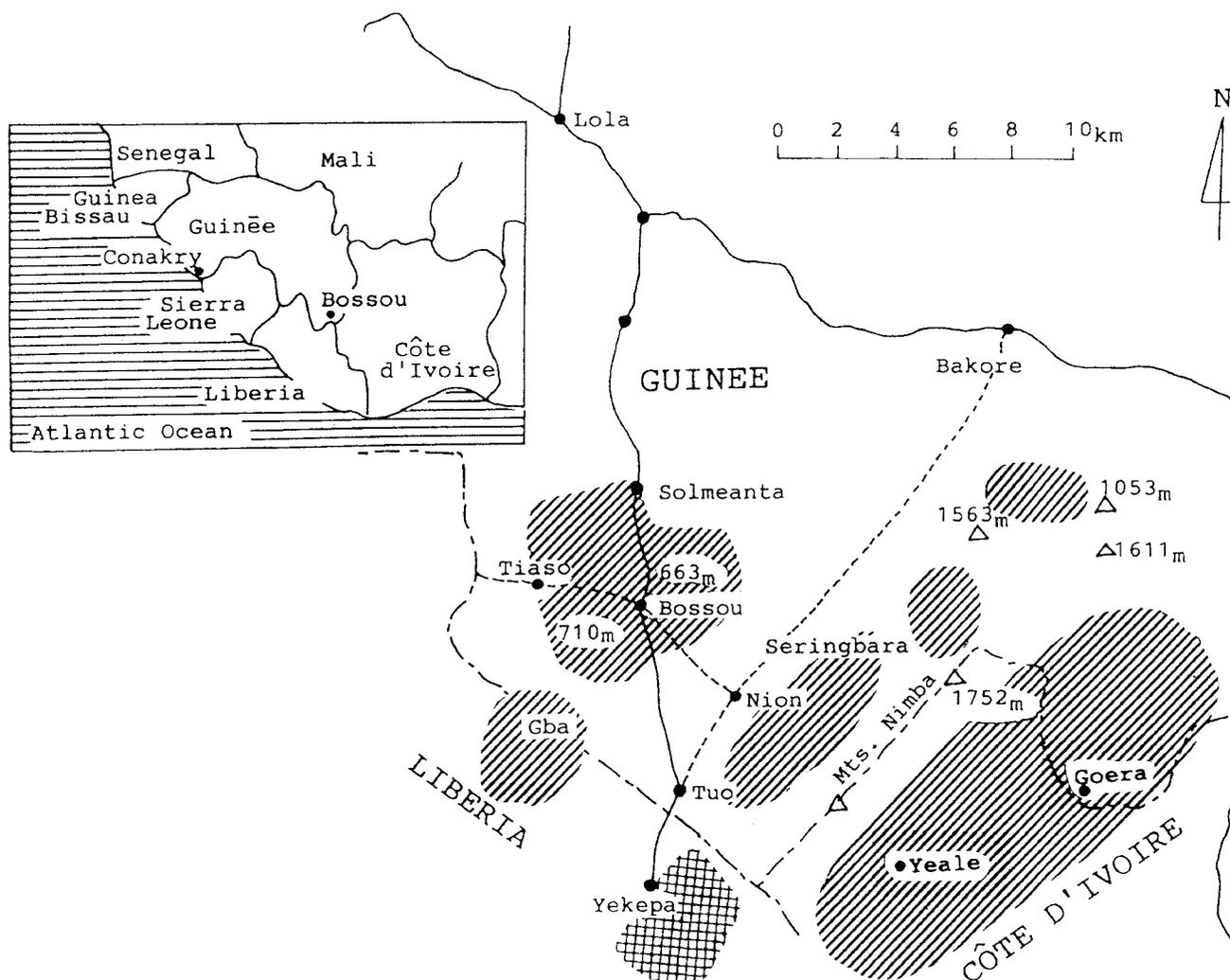


Fig. 1. Map of Bossou and Mt. Nimba. Chimpanzees had been confirmed at shaded areas, but disappeared from cross-hatched area after study began. Height above sea level is shown in meters.

stricted to the behavior of individuals only during the time when they are in a particular social group. Although there are some publications on the demography of chimpanzees, they come from only a few study sites, and the data are fragmentary.

This paper presents the demographic parameters of 26 years of chimpanzee research at Bossou, Republic of Guinea. Some restrictions on data collection, as occur at other study sites, are common. I compared the demographic parameters of chimpanzees at Bossou with other study sites, and compiled female and male life histories. I also focused on social structure, with special reference to local variation in life history and demography, particularly on the mechanism of the dispersal pattern, and the significance of the so-called "male bond."

STUDY SITE

Bossou is located in the southeastern periphery of the Republic of Guinea, West Africa, and at the border of Liberia and Ivory Coast, 7.39° N and 8.30° W. From late March–October it rains between

2,000–2,500 mm, and between November and early March it rains only 150–200 mm (Yamakoshi, 1998; Takemoto, unpublished findings). The home range of the Bossou chimpanzee group is 15–20 km², and it lies adjacent to villages and cultivated fields. The core area of the group, 6–7 km², consists of primary (c. 5%), regenerated (c. 25%), and secondary (c. 40%) forests on hills and in valleys, and cultivated (c. 10%) and abandoned (c. 20%) fields. Chimpanzees mainly forage in the forest, but sometimes come to the fields to take fruit (about 10% of feeding time; Takemoto, unpublished findings) and manioc. The core area of the chimpanzee group is surrounded by savanna with gallery forest or cultivated/abandoned fields. No adjacent group has an overlap of its core area with that of the Bossou group, but chimpanzees of an adjacent group(s) at Mt. Nimba are sometimes found and heard around the village of Selingbara on the peripheral part of the Bossou group's home range. The two villages are separated by about 5–6 km (Fig. 1).

Neither predators nor poachers of chimpanzees have been in or around Bossou since the intensive study began. Traps for catching cane-rats and squirrels, which occasionally caught infant or juvenile chimpanzees, were almost eradicated by 1990. Since 1976, no chimpanzee has died by being trapped. No monkeys occur in the core area of the chimpanzees, but *Cercopithecus* spp. are occasionally seen in the surrounding forests at the periphery of the home range of the chimpanzee group.

METHODS

Behavioral and ecological studies of the chimpanzees, with recognition of each individual, have been carried out intermittently since 1976 (e.g., Sugiyama, 1981). Except for 1978, 1981, and 1984, at least once a year one or more researchers who recognized each chimpanzee carried out short or long-term behavioral studies and recorded all chimpanzees living in Bossou. Since 1995, well-trained local assistants have been permanently engaged in field research and have continuously recorded each chimpanzee. Data in this paper are from 1976, the beginning of the study, until the end of 2001. The demographic records (birth, death, and presence in or absence from the Bossou group) used for this paper were collected by more than 20 researchers and two local assistants, who recognized each chimpanzee very well. Other data in this paper were collected by the present author unless otherwise stated. Recording of all individuals of the group can be done within a few days, although occasionally it has taken up to 10 days.

Infants (0–3 years) and juveniles (4–7 years) always stayed, and many times embraced a particular adult female. Adolescents (8–11 years) sometimes fed and traveled apart from any adult female, but much of the time they stayed with like-age juveniles. Thus the mother-offspring relationships could be easily recognized.

Many births were confirmed within a few months, but some were not confirmed for up to a year. The birth month and year of new infants in these latter cases was estimated by their body size, activity, and behaviors. For example, a new infant within a month of its life rarely leaves its mother's breast. Before 6 months it rarely rides on her back when traveling. Disappearances of Bossou chimpanzees were recorded from time of last observation. Some disappearances, however, occurred when there was no observer, particularly during the early stage of the study. In such cases, the month and year of disappearance were estimated as the halfway point between the last observation of the previous period and confirmation of absence in the following period.

Because observation was intermittent during the early stages of the study, there is the possibility of a few births and their early deaths between observation periods having been missed.

Between 1990–1995, for between 1–2 months a year, 10–20 bananas or oranges were given daily to

the chimpanzee group to facilitate field experiments. Baiting ceased, except for preparing some oil-palm nuts (*Elaeis guineensis*), after chimpanzees had become well-habituated to observers. Oil-palm nuts were deposited at the field experimental site in the center of the chimpanzees' core area as if they had fallen naturally.

At the beginning of the study in 1976, chimpanzee age was estimated by age-related features, behaviors, and other characteristics such as body size. Estimated age of the oldest offspring attached to each adult female was an important element in deciding the age of mothers. Consequently, a few mothers might have been estimated at slightly younger than their true age, because they may have had offspring unknown to observers when the study began.

RESULTS

Group size

Group size at Bossou has been maintained at around 20 throughout the study period of 26 years (Fig. 2). Prior to the maturation of one young male, the group contained only one fully grown adult male between 1978–1996 ("m. 12+y" in Fig. 2 includes a prime adult male of 12–15 years of age). In 1984, group size decreased to less than 18. Reduction in group size followed the *coup d'état* which occurred just after the President of the Republic of Guinea died in March 1984, and affected even remote villages like Bossou where villagers cut more forests than before and expanded cultivation to earn more money.

Due to the inland war in Liberia from the end of 1989, many refugees flooded into Bossou and adjacent villages on the Guinean foothills of Mt. Nimba. They cut forests for cultivation and building houses, and invaded the interior of the forest searching for and collecting food and other materials. As a result, chimpanzees lost food and feeding sites, as they were afraid of the noisy refugees and avoided them. On this occasion, reduction of group size stopped at 18.

On both occasions, I negotiated with village elders to stop cultivation in the chimpanzee core area, particularly from the higher part of the hills. I recommended that villagers use lower and wet lands, and supported them in doing so. Gradually, chimpanzee group size returned to the original numbers of 1976.

Reproductive success

Mother's age at first birth (primiparity). The sample size of primiparous females is only 5, because, as occurs in other chimpanzee populations (Gombe: Goodall, 1986; Mahale: Nishida et al., 1990), most young females disappeared around maturity, having possibly emigrated (see Survivorship and the Rate of Remaining in Bossou, below). One female (Pm) who first gave birth at 13.9 years was already about 9 at the beginning of the study, but

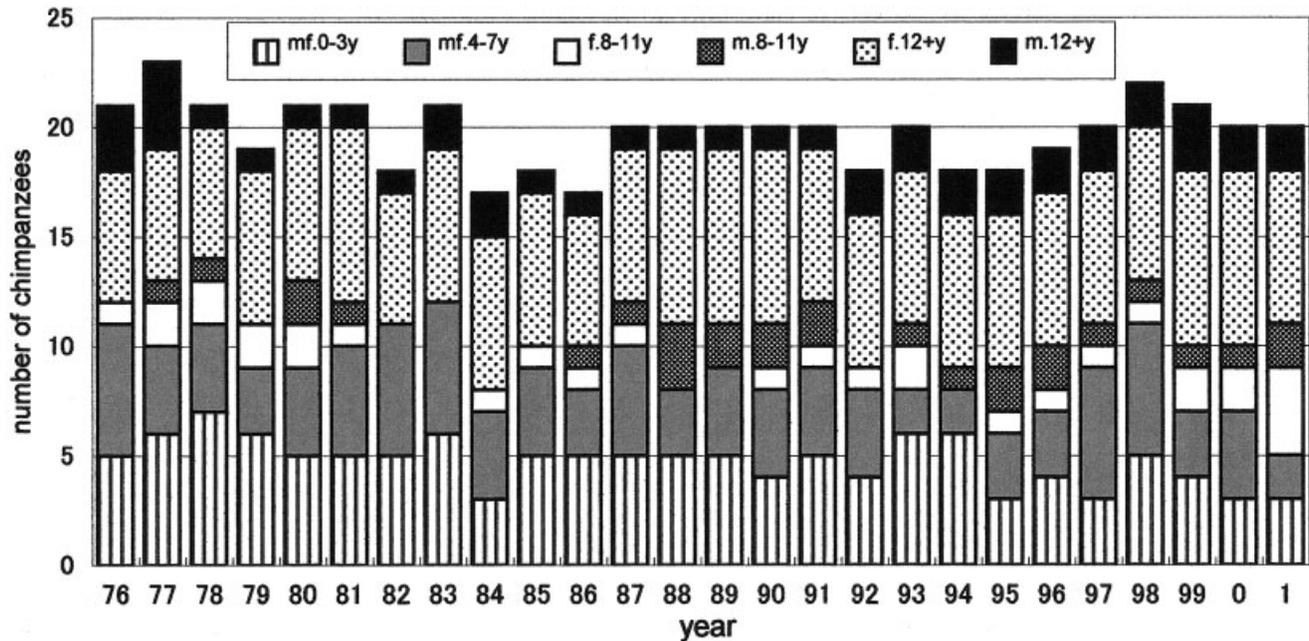


Fig. 2. Group size and age-sex composition of Bossou chimpanzees, 1976–2001. Figures for 1978, 1981, and 1984 are only estimates, as no observer was present to confirm group size and composition. m, male; f, female; y, age in years.

her age was an estimate only. Out of eight births for the other four mother-offspring pairs (Ki-Kk, PI-PK, Vv-Ve, and Ft-FK), five were confirmed between a few days and 3 months after birth, and the rest were confirmed after about a year. Most probably, estimated birth month and year for these latter cases were confined within a half-year, based on the features and activity of new infants when they were first found. By including the female who first gave birth at 13.9 years, the mean primiparous age at Bossou is 10.9 years (s.d. = 1.75). By excluding this female, it is 10.1 years (s.d. = 0.48). Even when estimate errors for the birthdates of both the mother and offspring for the four pairs are worked into the equation, the mean age of the mother at her first birth was not more than 11 years.

Thus, without exception, all females who were confirmed to have been born and stayed in Bossou until at least 12 years of age had their first birth at less than 11 years.

Age-specific birth rate. Age-specific birth rate was calculated (Fig. 3). One old mother (Fn) was estimated to be 41 years old at her last birth. She continued to exhibit ano-genital swellings when last observed at 44 years. After 39 years, the birth rate diminishes. Even including these older females, the mean birth rate between 9–41 years is 19.4% a year, and 16.5% in cases where infants survived more than 4 years ($N = 170$ female-years from 11 mothers, including 3 cases where infants were surviving but still less than 4 years old). If birth-rate data are pooled in 5-year groupings, females of 20–24 years are seen to give birth a little more than other ages, but no significant difference was found. The oldest

female (Ka), who was estimated to be 50 years old in 2001 and had not given birth since late 1976, was excluded from this calculation after her last birth.

From this calculation, chimpanzee females at Bossou who reach 9 years of age give birth 6.40 times and raise 5.45 offspring at least up to 4 years old, unless adult mortality is considered (see Survivorship and Rate of Remaining in Bossou, below).

In the early stages of this study when there was sometimes no observer present, a few births may have gone unrecorded if the infant died at less than 1 year of age. Were this the case, then the true birth rate may have been slightly higher and the infant survival rate may have been somewhat lower. However, the revised birth rate of infant survival (16.5%) is not affected by this.

Interbirth interval. The mean interbirth interval for a female was calculated as 4.6 years from the 22 infants born to six mothers. If only these cases where the immediately older sibling survived more than 4 years are considered ($N = 17$), then it is 5.3 years (s.d. = 2.26) (Fig. 4). The interbirth interval for a female was very regular in most cases where infants survived, and fell between 4–6 years, except in the case of one old female, Fn, who gave birth after an 11-year interval. If this exceptional case is omitted, as there was a possibility that Fn gave birth sometime during the 11 years but lost her infant before an observer could record it, then the mean interbirth interval becomes 4.9 (s.d. = 1.53) instead of 5.3 years for cases where the immediately older sibling survived. If the immediately older sibling was male, the mean interbirth interval was 4.9 years ($N = 8$, omitting the exceptional case), and if it

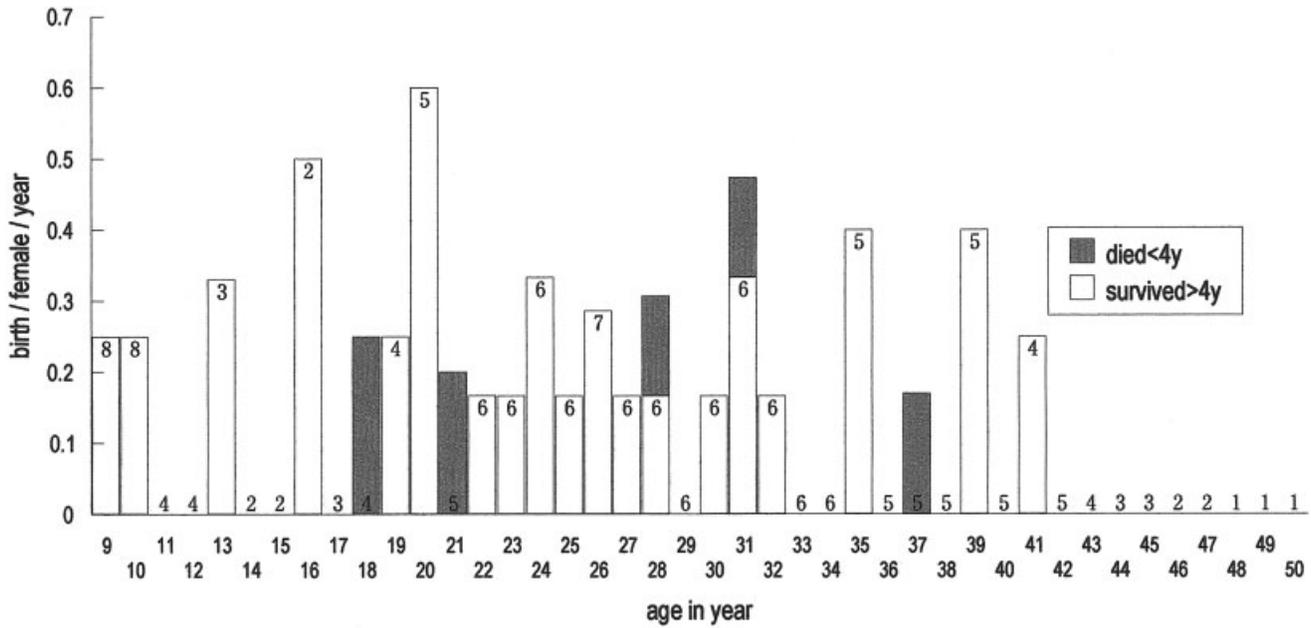


Fig. 3. Age-specific birth rate for Bossou chimpanzee females, 1976–2001. “Ka,” who did not give birth after late 1976, was excluded from 1977. Sample size (number of females) is shown in columns. died <4y or survived >4y, offspring who died before 4 years of survived more than 4 years after birth (note that two infants who are still less than 4 years old are included in “survived” category). Mean birth rate between 9–41 years old is 0.19 overall, but 0.165 if only infants who survived more than 4 years are analyzed.

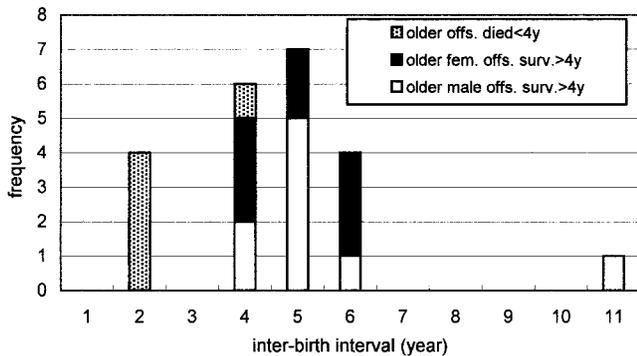


Fig. 4. Interbirth interval of Bossou chimpanzees, 1976–2001. Mean interbirth interval was 5.3 years if first offspring of a sibling pair survived for more than 4 years. It was 4.9, if exceptional case of an 11-year interval is excluded. Mean interbirth interval was unaffected by sex of first offspring of a sibling pair. y, years.

was female, the mean was 5.0 (N = 8). An infant’s sex rarely influences the interval to the next birth. Maternal age did not influence the length of interbirth interval (Fig. 5).

From the beginning of the study in 1976, seven adult and, at the time, an adolescent female were continuously present up to the end of 2001. As far as I could confirm, up until the end of 2001, each had raised at least 4.43 offspring (range, 3–5) to more than 4 years of age, and 2.57 (range, 2–3) to at least 8 years.

The oldest female (Ka), who had three offspring when I began the study in 1976, was at the end of reproduction. At that time, five other females already had one or two offspring. Two of these females

were still cycling at the end of 2001. Offspring who disappeared before I began this study and those who were yet to reach 4 years of age cannot, of course, be included in this calculation. Thus, the calculations of 6.4 births and 5.45 offspring up to 4 years, from the age of first and last births and interbirth interval, are adequate estimates for a Bossou female if she completes her life.

If the oldest female (Ka) had no offspring other than those she had when I began the study in 1976, and if her first birth was at 10.9 years old having the second and third births after 5.3-year intervals, then she was 47 years old in 2001. Although I placed her at 50, she is possibly older, as she finished reproducing in 1976 and was still alive in 2002.

Most offspring disappeared from Bossou after age 8. Unfortunately, their survival rate after disappearance could not be calculated.

During the 26 years of the study, 33 births were recorded, with a sex ratio at birth of almost 1, i.e., male:female = 48.5%:51.5%.

Survivorship and rate of remaining in Bossou

The rate of young individuals remaining in the natal group at Bossou was calculated (Fig. 6). The rate for both females and males was 80.0% for the first 4 years of life (infant stage); the other 20.0% died. Over the next 4 years (the juvenile stage from 4–8 years), the rate for females was 84.6%, and that for males was 64.3%. From birth to 8 years, the rates were 67.7% and 51.4% for females and males, respectively. However, over the following 4 years (the adolescent stage from 8–12 years), most natal females as well as males disappeared from Bossou,

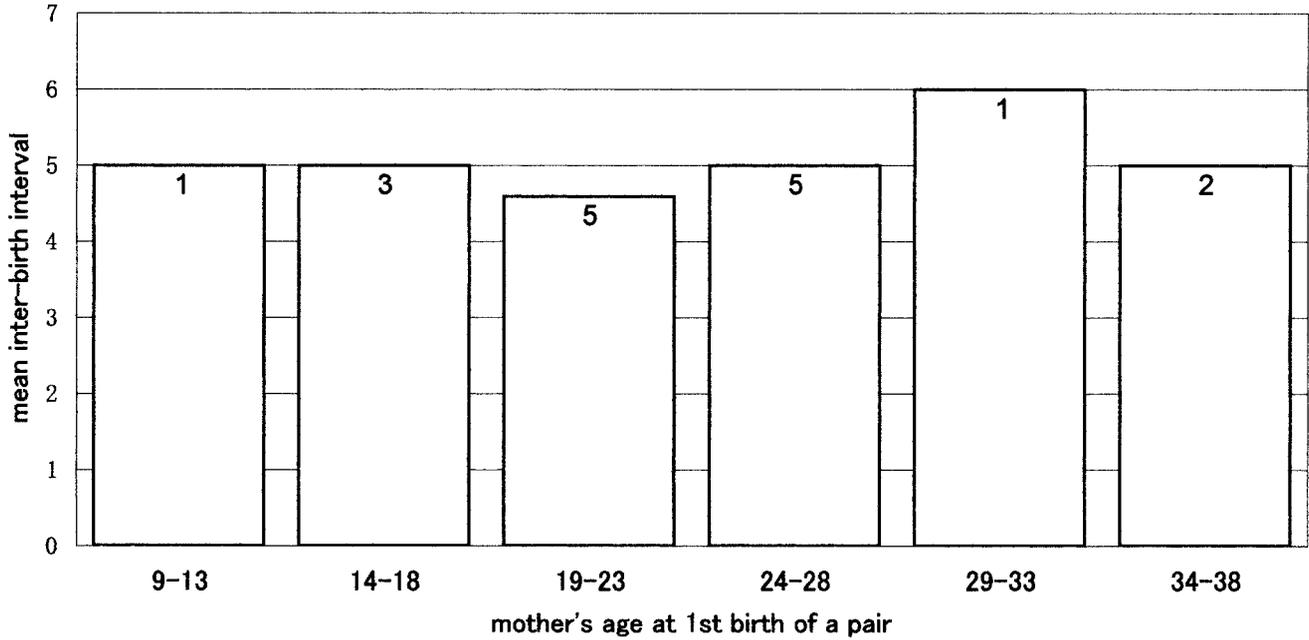


Fig. 5. Interbirth interval divided by mother's age when older sibling survived at least 4 years. Exceptional case of 11 years is excluded. Sample size is shown in columns.

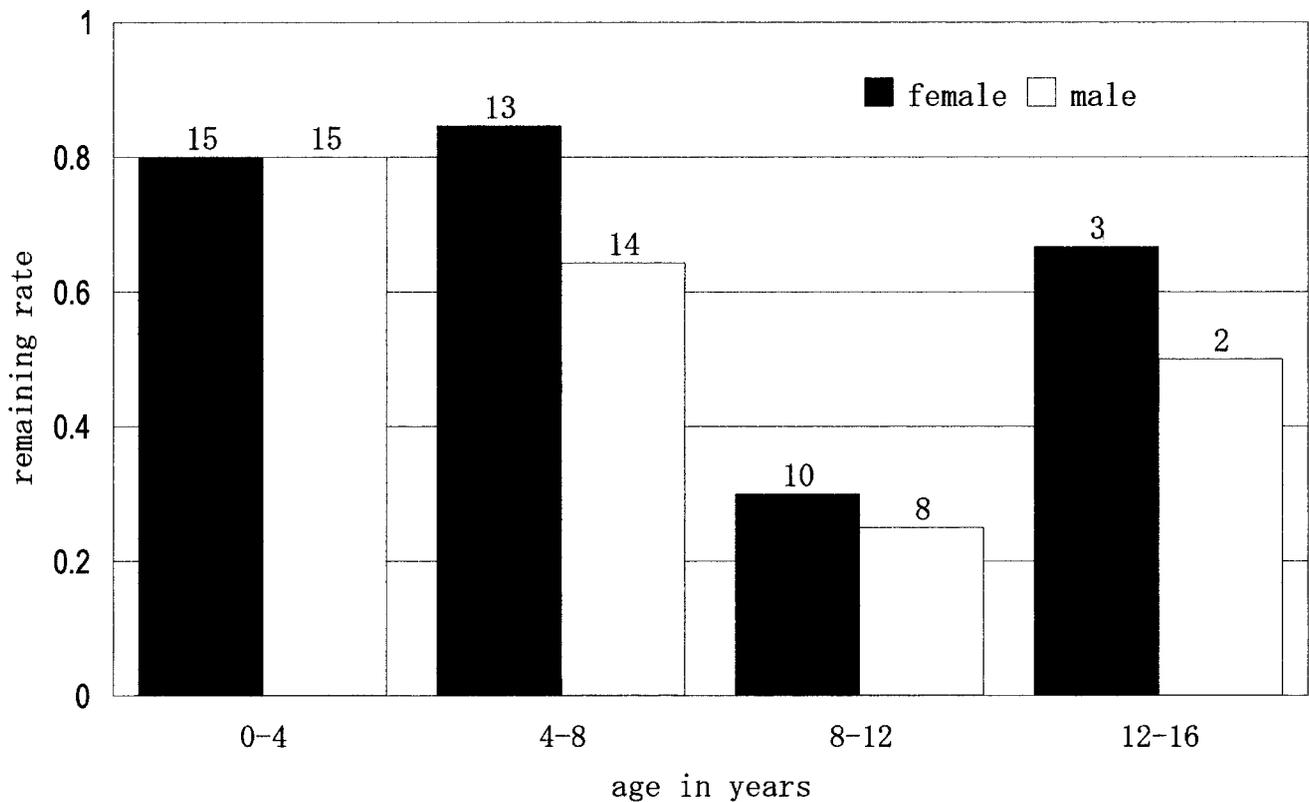


Fig. 6. Rates of remaining in Bossou from birth to 16 years, 1976–2001. Rate for prime adults, 12–16 years, is high, but sample size is small. Sample size is shown in columns.

with only 30.0% of females and 25.0% of males remaining. From birth, 20.3% of females and 12.9% of males remain to 12 years of age. Over the study period of 26 years until the end of 2001, only 3 natal

females, out of 17 who were born after 1976, and 2 males out of 16 reached adulthood (12 years of age in this paper) at Bossou. Of those 3 females and 2 males, only one male reached 15 years of age at

Bossou; all the others disappeared. The male who disappeared at 12 years (VI) was vigorous, without any outward sign of injury or sickness at the time (Takemoto, personal communication). Another male (PR) who was active disappeared at 11 years, after receiving repeated attacks from the alpha male (TA) (Sugiyama, 1999).

From these observations, it seems that at least some males and females emigrated from Bossou, even though no emigrant from Bossou, male or female, has been confirmed alive in the adjacent chimpanzee habitat because observation there is difficult.

Boesch and Boesch-Achermann (2000) claimed, without showing any evidence, that "the sudden disappearance of juveniles of both sexes from this small community [of Bossou] might unfortunately be related to external factors, such as poaching for food or providing medical centers with young chimpanzees." However, chimpanzees are special creatures to the villagers of Bossou, and they never allow people to kill them. In early 1976, before the long-term study began, a soldier who came from a distant region shot a juvenile chimpanzee. As the villagers had not allowed him to do so, the military commander had to relocate him (Jeremy Koman, personal communication). As the military generally do as they please, it is striking that the villagers stood up against this soldier.

For over 10 years between 1978–1996, there was only one full-grown adult male (TA) and, during this period, he was the alpha male for nearly 20 years. At the age of about 40, he was displaced by a young adult male of 17 years (FF). The deposed male is still in the group (as of the end of 2001), as the new alpha male has avoided attacking, threatening, or ousting the ex-alpha male. After the change in the dominance relationship between alpha and beta males, the ex-alpha male frequently worked at "herding" separated females and leading them to the larger party. He also sometimes visited Selingbara, at the foot of Mt. Nimba in the peripheral part of the home range, separating from the major part of the group with a few females.

The adult mortality rate cannot be calculated, as all adults and adolescents (≥ 8 years old) at the beginning of the study (both males and females) are still alive in the group, except for two full-grown males, who disappeared before the 1979 study period.

DISCUSSION

Reproduction and population

Except during the periods of deforestation, the population size of chimpanzees at Bossou was rather stable throughout the 26 years of the study. This suggests that the population may have been maintained at close to the environment's carrying capacity (there are few competitive fruit eaters other than a small population of hornbills). Age of first and last births, birth rate, interbirth interval, and survival

rate to maturity were calculated from the 26-year record. The age of first birth for females in Bossou is almost the same as that recorded in captivity (Smith et al., 1975; Udono et al., 1989; Yoshihara, 1999, personal communication), which is by far younger than that of chimpanzees from Gombe (Goodall, 1983), Mahale (Hiraiwa-Hasegawa et al., 1984), or Tai (Boesch and Boesch-Achermann, 2000). Chimpanzees of Gombe and Mahale are of the East African subspecies (*P. t. schweinfurthii*), whereas those of Tai and Bossou are of the West African subspecies (*P. t. verus*) (Table 1). Thus the difference between Bossou and other sites is more likely a reflection of environmental conditions than a subspecific difference.

Demographic and reproductive parameters for the chimpanzees of Bossou have the highest values for population growth among wild populations reported up until now. Lifetime reproductive success at Bossou was not only the highest but was also the most stable, as is evident from birth rates for ages between about 9–40 years, interbirth intervals, success in raising infants, and so on. Although sample sizes are small, demographic parameters for Bossou chimpanzees are similar to those of other African great apes such as bonobos (*P. paniscus*) (Furuichi et al., 1998, personal communication), gorillas (*Gorilla gorilla*) (Stewart, 1988), and captive chimpanzees (Table 1). Interestingly, differing from other nonhuman primates, great apes achieve similar reproductive success between captive and wild populations, though few samples are available at present. Not only ecological but also psychological factors between captive and wild conditions should be compared in the future.

In Bossou, much food is probably concentrated in a small core area. Fruits and other crops are available when food in the forest is seasonally scarce (Takemoto, unpublished findings). In addition, Bossou chimpanzees exhibit a variety of sophisticated tool-using behaviors (Sugiyama, 1997), and use tools particularly during nonfruiting seasons (Yamakoshi, 1998).

In contrast, the reproductive parameters of chimpanzees at Mahale, Tai, and probably Gombe seem indicative of population decline, as suggested by Sugiyama (1989) and Stanford (1998). As neither adolescent nor adult females present at the beginning of the study died during a period of 26 years, I could not estimate the usual mortality rate for mature females, and I assumed that all mature females give birth regularly until 40 years of age. Thus actual lifetime reproductive success must be less than the value presented in Table 2, if adult female mortality is to be calculated.

If the parameters at Mahale, Tai, and Gombe had held true throughout the long evolutionary process and over the entire distribution of this species, then *Pan troglodytes* would have already disappeared, as the intrinsic rate of increase is less than zero (Gage, 1998).

TABLE 1. Reproductive parameters of wild and captive African great apes

Species, colony, population	Menarche in years (range; n) ¹	1st parity years (range; n)	Interbirth interval years (range; n) ²	Infant survival ³		Species/Subspecies	References
				Male	Female ⁴		
Chimpanzee	Wild						
Bossou	8.5 (8–9; 5)	10.9 (9.7–13.9; 5)	5.3 (4–11; 17) ⁵	0.80	0.80	ver	Sugiyama, 1994; this study
Tai	10	13.7 (12.5–18.5; 7)	5.8 (4–10; 33)	0.6	0.6	ver	Boesch, 1997; Boesch and Boesch-Ashermann, 2000
Gombe	10.8 (8.5–13.5; 8)	13.3 (11.1–17.2; 28)	5.2 (3.3–7.8; 11)	0.659	0.758	sch	Goodall, 1986; Wallis, 1997
Mahale	10–11	14.6 (12–20; 10)	6 (4.5–7.3; 19)	0.36	0.49	sch	Hiraiwa-Hasegawa et al., 1984; Nishida et al., 1990
Chimpanzee	Captive						
Holloman AFB	8.8 (7.0–10.8)	10.5 (8.2–13.7; 17)				ver, tro, sch	Smith et al., 1975
Tama Zoo (Tokyo)	8.3 (6.8–10.2; 19)	11.5 (9.3–14.5; 16)				mostly ver	Yoshihara, 1985
Sanwa Prim Park	8.2 (7–11; 5)	10.0 (9–11; 6)	4.2 (?; 8)			mostly ver	Udono et al., 1989
Whole Japan Zoo	8.3 (?)	11.6 (5–37; 127)				mostly ver	Yoshihara, 1999
Bonobo	[Wild]					<i>paniscus</i>	Furuichi et al., 1998; personal communication
Wamba			4.8 (1–9; 28)				
Gorilla	[Wild]						
Kalisoke		10.2 (9–13; 8)	3.9 (3–4.9; 22)			<i>beringei</i>	Fossey, 1982; Stewart, 1988
Kahuji		10.6 (9.1–12.1; 18)	4.6 (3.4–6.6; 18)			<i>graueri</i>	Yamagiwa, et al. 2001
Virunga		10.1 (8.7–12.8; 16)	3.9 (3.0–7.3; 16)			<i>beringei</i>	Watts, 1991
Gorilla	[Captive]						
Euro-American zoos		9.4 (6–19; 44)	4.2 (2.3–6.4; 16)				Sivert et al., 1991; Kirschofer, 1987

¹ Judged from maximum sexual skin swelling in wild.

² Only cases in which older offspring of a sibling survived with its mother.

³ Infant survival rate at 4 years of age.

⁴ ver, *verus*; tro, *trogodytes*; sch, *schweinfurthii*.

⁵ If an exceptional case is omitted, 4.9 (4–6; 16).

TABLE 2. Reproductive success of wild chimpanzees at four study sites¹

Research site	Age of primiparity ①	Survival to primiparity ②	Inter birth interval ③ ⁴	Lifetime reproductive success ⁶	References
Bossou	10.9	0.58	4.6	4.25	This study
Tai	13.7	0.22	4.65	1.46	Boesch and Boesch-Ashermann, 2000
Gombe	13.3	0.46 ²	4.3 ⁵	3.32	Goodall, 1983; Wallis, 1997; Pusey et al., 1997
Mahale	14.6	0.28 ³	3.7	2.20	Nishida et al., 1990

¹ Sample size of ② for Bossou is 122 female-years from 18 individuals; for Mahale, >92 (male + female). See Table 1 for sample sizes of ① and ③.

² Survival rates for juveniles and adolescents were applied to those of Bossou.

³ Survival rates after 8 years were calculated from those of the previous age class.

⁴ Interbirth interval includes early infant death.

⁵ Interbirth interval of Gombe is an estimate as 1/3 of an older infant of a sibling died at 1.5 years. Assumption: all mature females regularly give birth until 40 years.

⁶ Lifetime reproductive success was calculated as: $[(40 - \text{①})/\text{③}] + 1 \times \text{②}$.

In spite of such favorable reproductive conditions, the carrying capacity in Bossou is limited, and group size most likely cannot expand far beyond present numbers. Thus, some individuals (young active animals) must, as in many other mammal species, disperse. During times of deforestation when the population decreased (1984–1986, 1992–1995), vulnerable infants (0–3 years of age), juveniles (4–7 years), and active adolescents (8–11 years) were affected more than other age-sex classes (see Fig. 2). In these years, young active animals between 12–15 years might have had no choice but to disperse. Thus, group (or population) size and the dispersal pattern of animals may be directly influenced by the carrying capacity of the habitat.

Female life history

Young mature female emigrants may be accepted into adjacent groups and produce offspring, as seen in other populations (Goodall, 1986; Nishida et al., 1990; Boesch, 1997). Most adolescent and young adult females disappeared, and perhaps some of them emigrated from Bossou. In contrast, females already mature or nearly mature at the beginning of the study have remained in Bossou over the last 26 years, and all were still living there until the end of 2001. Thus it seems that females who exceeded the carrying capacity of Bossou and consequently emigrated were not established ones, but younger, more active ones.

The mothers of many mammal species, particularly those of a solitary nature, stay in their established territory or home range, and it is the offspring that disperse (e.g., wood mouse: Ohnishi et al., 2000; feral horse: Asa, 1999; wild boar: Hirotani and Nakatani, 1987; canid: Koopman et al., 2000; primates: Pusey and Packer, 1987; Chepko-Sade and Halpin, 1988). A reduction in the number of females due to death from old age or sickness may be counterbalanced by immigrants, as seen in other populations, but over the last 26 years, we have not found any females in or around Bossou other than the identified group members. The replenishment of females might also be accomplished through young natal

ones not emigrating. Natal females can be expected to remain for life, as four of them gave birth in their group.

At the beginning of the study in 1976, there were seven adult or adolescent females in Bossou. We discovered through field experimentation that only one of them knew of coula nuts (*Coula edulis*), which are common in Mt. Nimba, an adjacent chimpanzee habitat (Matsuzawa et al., 2000). This suggests that the other six adult females were not immigrants but were probably born in Bossou, because there is no other adjacent chimpanzee population that is unfamiliar with coula nuts. Considering this fact, some natal females can remain for life in Bossou, particularly those who give birth in their natal group located in Bossou.

Data from Bossou suggest that in raising 5–6 offspring at least up to 4 years old, females may live 50 or more years.

Male life history

Adolescent and young adult males also must have dispersed, except for the one who remained in the group. He helped to maintain and guard females by accompanying the alpha male when the latter became old. Before the long-term study began at Bossou, poachers occasionally came from out of the village, and the chimpanzee group had three adult males until 1977, presumably as a defending strategy against poachers and human strangers. Because chimpanzees were shy and were afraid of human strangers, humans and chimpanzees kept a great distance from each other, though the villagers treated the former as a kind of special creature that looked like humans. After our long-term study began, a poaching ban was strictly enforced, and the chimpanzees gradually became accustomed to villagers. Following this, an old alpha and a young adult male in 1976–1977 disappeared, and only the beta male remained in the group (Sugiyama, 1981). In such a small group with few enemies and no conspecific competitors, young mature males may be able to remain in their natal group only when the alpha male becomes old or weak and gradually loses

his alpha status, as occurs in mountain gorilla groups (Yamagiwa, 1987).

I hypothesized previously (Sugiyama, 1999) that young growing males are not collaborators with the alpha male in territory defense, but are simply competitors for resources in a semi-isolated condition where no adjacent group has its core area overlapping. Consequently, adolescent and young-adult males have to emigrate to an adjacent habitat, whether or not they receive direct attacks from the alpha male (Sugiyama, 1999). Even if they are not accepted into another group, they will have the opportunity of siring offspring outside of their natal group. Sugiyama et al. (1993) and Gagneux et al. (1997) concluded by DNA analysis that males other than those of a particular group can mate with females and produce offspring. Although Gagneux et al. (1997) were recently refuted (Constable et al., 2001), extragroup mating is still expected to occur around Bossou because the periphery of the home range, the foot of Mt. Nimba, is exempt from patrol by group males. In fact, genetic relations between the chimpanzees of Bossou and Mt. Nimba are suggested to be close (Shimada et al., 2001). Considering that only one female of Bossou knew the behavior pattern of the Mt. Nimba population, i.e., *Coula edulis* nut-cracking (Matsuzawa et al., 2000), a close relationship between the Bossou and Mt. Nimba populations may not have been established and maintained only by female migration, but also by male movement.

More recently, Vigilant et al. (2001) reexamined the paternity of Tai chimpanzees, and found that extragroup paternity was less than Gagneux et al. (1997) expected (50%), but more than Constable et al. (2001) statistically calculated (0%), i.e., at least 17%. Sugiyama (1999) cannot be refuted by statistical methods, as an offspring of the Bossou group showed an amplified DNA band which was absent in its mother and the group male.

In and around Bossou, there have been neither poachers nor predators since the beginning of the study. This must surely contribute to why the alpha male does not need other males as collaborators. Group hunting of middle-sized mammals by chimpanzees, particularly by a group of males, is well-known at other chimpanzee habitats (Boesch and Boesch-Achermann, 2000; Uehara et al., 1992; Wrangham and Bergamnn-Riss, 1990). A lack of middle-sized mammals suitable for group hunting, such as red colobus (*Procolobus badius*), may be a subsidiary reason for the alpha male not needing male collaborators. Moreover, the small number of females due to restricted favorable habitat further limits potential male numbers (Mitani et al., 1996; Nunn, 1999).

These observations suggest that an alpha male chimpanzee accepts other males in his group and forms so-called "male-bonds," mainly to defend resources (his territory with its food and females) against neighboring conspecific competitors and

predators (including poachers). Male bonding may also be effective in obtaining meat through cooperative hunting. Such necessities must contribute to why chimpanzees in many habitats form a "male philopatric society," making them somewhat of an exception compared to most mammals, whose males disperse far more frequently than females (Greenwood, 1980; Janson, 2000).

Wrangham (1987) emphasized that chimpanzees (and common ancestors with humans) have hostile and stalk-and-attack intergroup relationships. Hence, he suggested, closed social networks among males within a group are necessary. However, there are still a few problems in explaining the special character of chimpanzees. In many nonhuman primate species, a male bond for the defense of resources is not usually based on kin-selected benefits (Stanford, 1998). Until now, there has been no reasonable explanation as to why only chimpanzees selectively need the "kin-related male bond" and "all-male philopatry." Perhaps large body size and aggressiveness make aggressive contact with conspecific competitors or predators potentially more fatal. More trusted kin-related collaborators may be needed for alpha male chimpanzees, as is the case for Serengeti lions (Bertram, 1978). However, a few examples of male immigration at Bossou (Sugiyama and Koman, 1979) suggest that a "nonrelated male bond" is also possible for chimpanzees. Male immigration at Bossou and evidence of extragroup siring at Bossou and Tai, though less frequent, may help to solve the problem of intragroup incest when natal females remain in the group.

Hohmann (2001) observed that some bonobo (*Pan paniscus*) resident males disappeared from, and strange males joined, a community (group) at Eyengo, near Lomako, Republic of Democratic Congo (Zaire). At first sight, the resident males were aggressive to strange males but gradually became tolerant. Immigration took place over a year, and at last new males succeeded in mating with community females. Hohmann (2001) suggested that the male transfer occurs when adult sex ratio (female/male) is high. Considering this study, males who left Bossou might be able to mate with females and join a neighboring chimpanzee group, though its sex ratio is not known.

Nishida et al. (1990) and Boesch and Boesch-Achermann (2000) definitely considered all disappeared adult and adolescent males as being dead and not emigrated. However, some can be expected to have emigrated. Although they believed that a high adult sex ratio (female/male) depends on male-biased mortality, the factors of sex difference of mortality are not yet clear.

Some authors emphasized that a male philopatric and female dispersal society is the common character of both African great apes and humans as a patrilocal or patrilineal society (e.g., Itani, 1985; Wrangham, 1987; Pusey, 2001). However, the male philopatric and female dispersal society of humans

is related to factors such as the succession of property in families and/or the political use of daughters for establishing or maintaining a special and strong bond between other families or communities. The exchange of daughters in receipt for money was more common among traditional societies, as daughters were considered paternal property. Thus, traditionally, female dispersal in humans had little to do with strategy-making by females.

In contrast, dispersion of female African great apes is self-determined, perhaps for their own cost and benefit. Many human males, even in agricultural societies, disperse, and only a few sons in a family are actually philopatric (Towner, 1999), usually because the parents' property is inherited by just one son. Consequently, kin-related male-bonding and female dispersal in the great apes must be considered and analyzed separately from human societies. Wrangham (1980) discussed and made clear the differences between the female-bonded (related) group and nonfemale-bonded group. However, the "all-male philopatry" of chimpanzees, which is a kind of nonfemale-bonded group, is very special among mammal and human societies. Although no author has focused attention on it, the exact maturing rate and maturing number of natal males must be presented. This must be the most important facet of the special character of chimpanzee social organization and reproduction yet to be explained.

Although the relationship between ecological adaptation to the environment, social organization, and its maintenance mechanism is one of the most important topics of socioecology (e.g., Johnson and Gaines, 1990), it has not been a common topic in studies of chimpanzees. Further studies are needed to understand the unique male bond and all-male philopatric society of chimpanzees to determine if these really are fundamental characteristics of chimpanzees.

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