

Reproductive Parameters and Group Extinction of Chimpanzees at Bossou, Guinea

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Abstract: Fifty years have passed since we started our field studies of the behavior and ecology of western chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. Although the group was small, 21 individuals at that time, continuous scientific monitoring and a substantial amount of demographic data were recorded over the years. Here, we calculate the age of first and last birth by females, interbirth interval, reproductive success, number of years alive after the last birth, and longevity. The results show that the average female reproductive success was greater than 2, which should suggest that the population was expanding. However, from 2003, group size began to decline after an apparent epidemic disease killed 5 or 6 individuals. From that point, the population continued to decrease from 19 to only 3 individuals remaining in 2024. These three individuals consisted of two adult males and one old post-reproductive female, leaving no possibility for growth and recovery as a reproductive unit. In addition to the loss of many members to disease, an important reason for the group's decline is that most male and female members born in Bossou after 1976 disappeared around the age of sexual maturation, and only a limited number of chimpanzees temporarily immigrated into the group. Unfortunately, the reproductive fate of the young individuals who disappeared could not be determined. As for the scarcity of immigration into the group, we can only speculate that chimpanzees from the adjacent region of about 6 km were too shy to approach the group, perhaps due to a combination of factors including its proximity to research staff, the noise from the adjacent Bossou village, and the savannah and roads separating them. Our study provides another example of the risk over-habitation poses to the survival of wild chimpanzee populations.

Key words: primiparous age, inter-birth interval, last birth, longevity, emigration, immigration

INTRODUCTION

The chimpanzee is an endangered species, with a decreasing number of wild populations and individuals. A key reason for this decline is the reduction of suitable habitat due to deforestation and forest fragmentation. Another problem for chimpanzees, as well as for most other wildlife species, is the proximity and potential conflict with humans caused by the advancement and invasion of agricultural and industrial development in their native habitat. In such environments, continued study of small populations of chimpanzees in the fragmented habitat is badly needed.

Many studies of wild chimpanzees are limited to the study of intelligence, social behavior, and social organization. However, for conservation efforts biological research is essential, particularly as it relates to reproductive activity.

Calculating reproductive success in terms of the number of female offspring produced by a mother is useful for determining the growth rate and sustainability of a population of animals (Bronikowski *et al.* 2016). If the average number of female offspring that survived to their mother's age equals one, the population size remains stable. If it



Figure 1. Bossou male, Fanwaa, grooming his mother, Fanle. Photograph by G. Ohashi.

is more than one or less than one, the population is expanding or decreasing, accordingly (Wilson 1975). Thus, calculating reproductive success is important for our ability to predict a population's future.

The long lifespan of chimpanzees requires the inter-generational collaboration of researchers following a single population across multiple generations. However, many female chimpanzees spend most, if not all, of their reproductive lives outside their natal population, making it difficult to accurately measure reproductive success (Goodall 1986; Nishida 2012). Given these constraints, we calculated the reproductive success of individual females where possible and supplement it with additional information relating to population dynamics at Bossou, Guinea.

MATERIALS AND METHODS

Environment

A small group of western chimpanzees (*Pan troglodytes verus*) of Bossou, Lola Prefecture, Republic of Guinea, West Africa, has been studied for their behavior and ecology since 1976 (Figure

1). Bossou village is located at 7°39'N and 8°30'W, about 500 m above sea level. The core area of the chimpanzee group is about 15 km² around five small hills: Gban, measuring 704 m; Guei, 663 m; Bouton, 507 m; Ueyaton, 600 m; and Tonzerou, 560 m asl (Figure 2) (Sugiyama & Koman 1979). The road to the north is connected to the adjacent village Solomeanta and the town Lola surrounded by savanna or cultivated fields. To the west are forest and scattered villages, e.g., Tiaso and Gba, and to the south is grassland and villages (Tuo and Yekepa) and the frontier of Liberia. On the east side are savannah, the villages of Selingbara and Nion, and Mt. Nimba, where there are other wild chimpanzee populations.

Between Nimba and Bossou the land was covered by grasslands which were burned every year during the study period. Villagers did not know whether the fire was natural or artificial. One of our members tried to study these events starting in 2000, however, his personal project (Green Corridor) failed until 2020 when the project was taken over by the government. Until now, the project has not progressed.

This area was primarily tropical rainforest and savanna, but nearly 80% was cultivated fields and/or

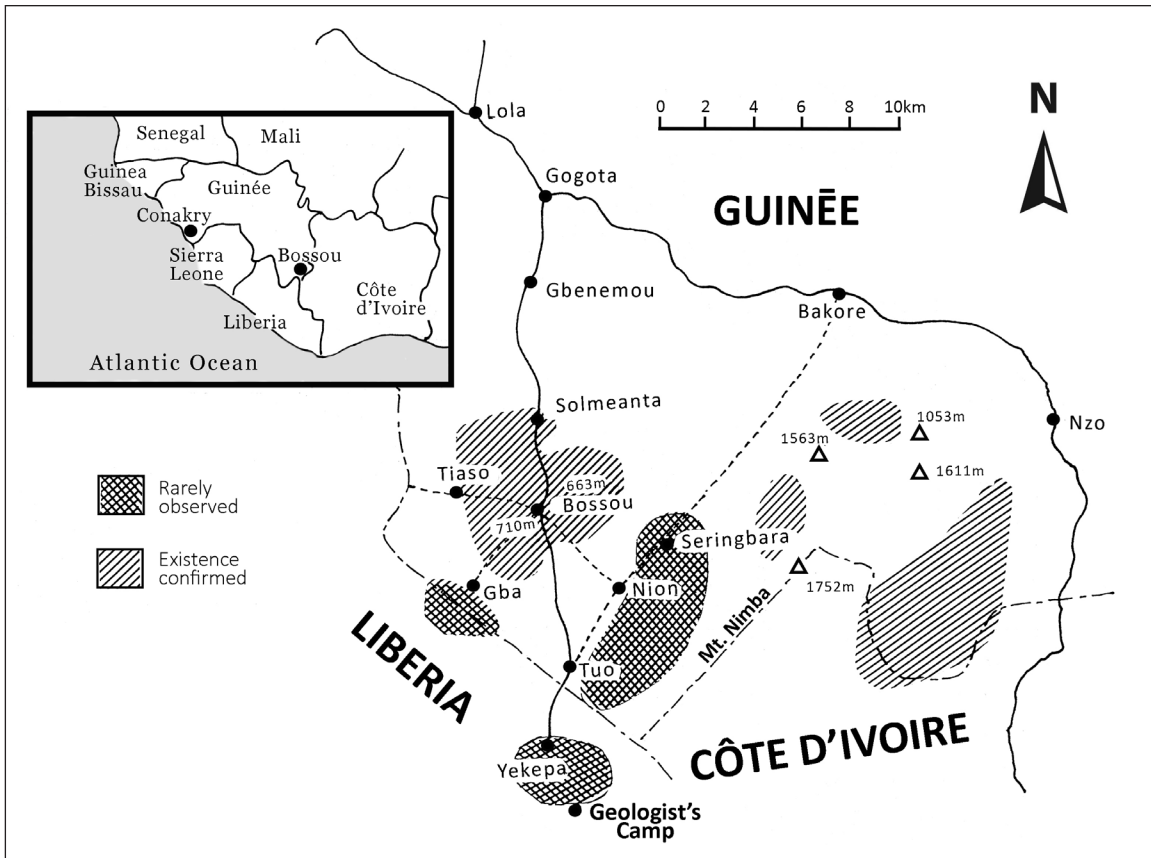


Figure 2. The group often divided into two or three parts and a part sometimes traveled far from the other parts. Then the out-line of the group's range is not clear and obscure. Confirmed area around Bossou village is the core-area and the total area of the home-range can't be shown in this map. Other confirmed areas were observed or heard vocalization by us or our local assistants though the group was not identified.

secondary forests of various stages after abandoned shifting cultivation (slash and burn agriculture). The remaining 20% or more was natural forest on mountain slopes, not suitable for cultivation but easily navigable by wildlife and humans. The forests and fields form a shifting fragmented and mosaic habitat. The forest and village conditions changed little until 1990-2000 because the President of Guinea closed the country to all but those from socialist countries and there were no social, cultural, or economic exchanges with other parts of the world. We rarely encountered villagers in the forest, at least until 2000.

Feeding, Competitors and Other Populations

The main foods of chimpanzees are fruits and young leaves of trees (Sugiyama & Koman 1987). Occasionally the group moved into agricultural fields to feed on bananas, oranges, papayas, young

pineapples, and other crops, though females usually avoid coming out to open ground and wait at the forest edge when adolescent and adult males forage in the fields. The crop feeding occurred more frequently after 2010. There are only a few mango trees in the forest, and chimpanzees regularly feed on these fruits. Occasionally, they also dig out the root of cassava (Sugiyama & Koman 1979, 1987). They take bird eggs from their nests and capture insects and small mammals, such as pangolins (Sugiyama & Koman 1987; Hockings *et al.* 2010). Although there are many wild chimpanzee populations within 100 km around Bossou, none of them were provisioned.

There are no natural predators in and around the core area of the chimpanzees of Bossou. Until recent years, villagers never harmed chimpanzees, though people chased them off from their agricultural fields. Chimpanzees were regarded as sacred animals by villagers who kept their distance from the apes (Yamakoshi 1999). However, since the early 2000s,

habituation of the chimpanzees has progressed. YS, as the director of the research field, informed researchers to maintain a set distance of 7-10m from the chimpanzees. However, some visiting researchers began to observe them closer than this against our direction. An adolescent and young adult male chimpanzee became habituated to researchers and villagers and began visiting cultivated fields in the forest and village gardens to take papaya fruits (Hockings 2011). After 2015, male chimpanzees were reported to attack and hurt village children who were carrying bananas to the village from their cultivated fields. These behaviors were rarely seen before the years 2000-2010.

The only feeding competitors of chimpanzees are one hornbill species (*Ceratogymna atrata*) and other birds and squirrels. Occasionally, two monkey species, the green monkey (*Chlorocebus sabaeus*) and spot-nosed monkey (*Cercopithecus petaurista*), were observed in the range of chimpanzees, but their densities are low.

In the Nimba mountains, more than 6 km east of Bossou, the presence of other groups of chimpanzees has been confirmed (Humble 2011a; Koops 2011). In the Liberian territory, south and southeast of Bossou, chimpanzee groups also exist within several kilometers (Sugiyama 1989; Ohashi 2011). From 1976, when the long-term study was started until 2002, the group size of Bossou chimpanzees remained at approximately 20 (range: 16-23; average: 20.5 individuals) but decreased due to fatalities from the spread of a flu-like infectious disease (Humble 2011b). From November 2003 to March 2004, six individuals disappeared: two old females, two 2-3 year old infants, and two 13 year old females. We were able to confirm that the first 4 individuals died, but we are not certain if the last two young adult females died or emigrated. The population continued to decrease (Sugiyama & Fujita 2011) until only three individuals remained in 2024.

The human population has grown, and the village borders slightly expanded since 1990-91, but the size of the forest and cultivated area remained stable (Y. Sugiyama, pers. obs.). The main reason for the population increase is the inland war that started at the end of 1989 when an anti-government rebellious troop rose in Cote d'Ivoire and invaded Liberia. Refugees, mostly merchants or mining laborers, came to Bossou to escape the conflict (Sugiyama 2008). The market expanded and became noisier, but the cultivated fields saw only modest changes (Y. Sugiyama, pers. obs.).

Data Collection

An expedient way of collecting data on individuals at different ages is to combine and calculate the mean values of same age class members. The main caveat of doing this for our study is that, at Bossou, most female and male chimpanzees disappeared when they were adolescent or young adults. This made it difficult, if not impossible, to determine whether their exit from the group was due to death or emigration. Under these constraints, we attempted to calculate reproductive parameters in each age class whenever possible.

Demographic records of Bossou chimpanzees have been collected every year since 1976, until 2011, except for 1978, 1981, 1984. After 2012, data collection was carried out by our trained local assistants. The age of individuals in the group in 1976, when the study started, was estimated. Age estimation of chimpanzees was made based on experience of YS at Budongo, Uganda, and on published data from captive subjects at Primate Research Institute, Inuyama, and Arnhem Zoo, Netherlands. The number of offspring and their body size were important for age estimation of females as well as notation of their behavior and physical features.

Approximate age was also determined based on the following indicators: a mother always carries her new infant near her breasts until it reaches a year old or more. When travelling, she carries it ventrally, often supporting with a hand for as much as two years. As an infant develops it begins to ride on the mother's back grasping the hairs of her neck and flank (Sugiyama 2008). Until five years of age, a chimpanzee infant spends most of the time near its mother. Even when they can walk independently of the mother, they rarely move more than several meters away. Up to about five years of age, these young chimpanzees are classified as infants. After about five years of age, they are classified as juveniles, and (males in particular) will begin to travel apart from their mothers at least occasionally. The ages of all other individuals are known.

RESULTS

First and Last birth, Longevity, and Interbirth Interval

The average age at first birth was 10.2 yrs (range = 8-13 yrs, N = 5). A nulliparous female who disappeared at 14 years of age is not included in this calculation.

The average age of last birth for seven females was 35.7 yrs (range = 26-51 yrs, N = 7). Six of these were already full-grown adults with one or two young offspring when the research started, taking into consideration possible errors in estimating age. The average estimated age of the six females at death was 55.8 yrs (range = 49-66 yrs, N = 6). One female of 67 yrs (estimated) was still alive in 2025; the average longevity of the above seven females is therefore more than 57.6 yrs.

The average interbirth interval was 4.56 yrs (range = 2-11 yrs, N = 25). If the four cases where the offspring died before 5 years of age are excluded, which is the standard acceptable method of calculating interbirth interval, the average IBI increases to 5.04 years (range = 3-11 yrs, N = 21). The latter IBI will be used in the following sections.

Infant birth and death

During the 50 years between 1976 and 2025, 40 chimpanzees – 23 females (57%) and 17 males (42%) – were born. Infant deaths at less than 5 years of age were 6 females (26.1%) and 4 males (23.5%). In this calculation, infants present in Bossou when the study started were not included. There was no statistically significant difference in sex (Fisher's exact test, two-tailed, $p = 1$). One four-year-old female who disappeared with her mother was assumed to have emigrated and was not included in this calculation.

Disappearance of Juveniles, Adolescents, and Young Adults

Out of 54 juveniles, adolescents, and young adults (5-15 years old), 29 disappeared (females = 16 of 31, 51.6%; males = 13 of 23, 56.5%). There was no statistically significant sex difference (Fisher's exact test, two-tailed, $p = 0.77$; Figure 3). Many of these disappearances occurred suddenly. In all cases the individuals were never sighted again, so it was not possible to determine whether they emigrated or died.

At the start of the study there were 7 adult females in the group: 6 were fully mature with infants and one was close to achieving maturity. All females born subsequently, except for two, disappeared before turning 16 years old.

Among 22 male infants present at the start of, and throughout, the study period, 5 (22.7%) disappeared before reaching the age of 5. They were presumed dead since all the mothers were still living in the group. Excluding these five infant deaths, 13 of 17 (76.5%) disappeared before reaching the age of 17 yrs. Only one male was known to have survived for more than 30 years in the group. Two-thirds of the males who reached 5 years of age disappeared before reaching full-grown adulthood. YS observed two such cases, one, an 11-year-old male who sustained a minor injury to his calf disappeared in November 1991, and another, a 12-year-old who was last seen

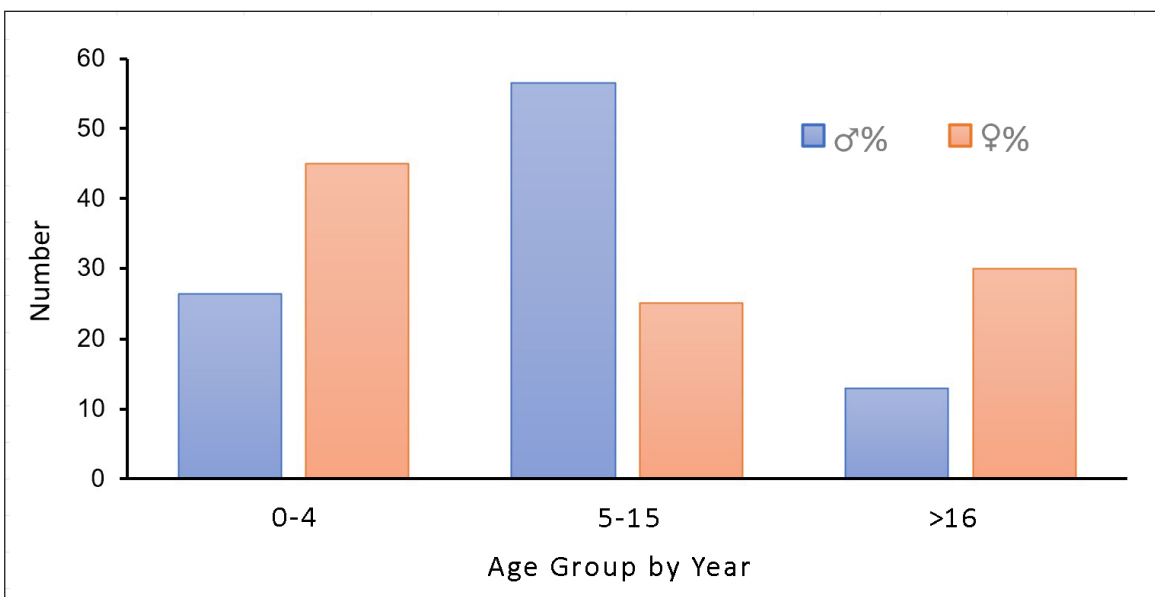


Figure 3. Age class (in years) of individuals that disappeared from the Bossou chimpanzee group.

in August 1999. They were probably not dead, at least, immediately after they disappeared (Sugiyama 2008). Mortal remains of chimpanzees of more than 5 years of age were rarely found in the core area.

Between November and December 2003 when a flu-like disease was spread among many chimpanzees, two old females, two 2-3 year infants, and a 13-year-old female disappeared. The old females and the infants were likely deceased, but it remains unclear if the younger female emigrated or died. In March 2004, another 13-year-old female disappeared but we do not know if her disappearance was related to the flu-like disease.

Immigration

Throughout the 50-year study, only two strange males, one older than 30 years and another less than 20, joined the group in the early stages of the study. The older male established friendly relations with the group males, but females kept a distance of more than 10 m. He stayed for only 20 days, then disappeared again. The younger male stayed about one year, formed typical social bonds with other members, then disappeared (Sugiyama & Koman 1979). It was not known if they were born in Bossou or another forest. No other immigration by males has been observed. No immigrant females were observed throughout our entire study period.

Only seven males 15 years of age or older have lived in the group, except for the above mentioned two males who temporarily joined in the early years. Five males of known age disappeared, ranging in age from 15 to 56 yrs (average = 27.8 yrs, $N = 5$). Two full-grown males were still alive in Bossou as of 2025.

Longevity

Six out of seven adult and sub-adult females from the study population were dead or presumably dead at an average of 55.8 years of age (range = 49-66 yrs, $N = 6$). This number may increase as the last remaining female was still alive as of 2026 and is estimated to be 67 years old. Thus, the longevity of matured females can be stated as more than 57.6 yrs. As the last birth was on average at 35.9 years of age, Bossou females can be said to continue to live for a further 21.7 years until death.

Reproductive Success

On average, female chimpanzees of Bossou became sexually mature at around nine years of age,

gave birth to their first offspring at 10.2 years, and continue to give birth thereafter every 5.23 years until the age of 35.7 years on average. Throughout their lives they sired 4.88 offspring with 2.66 (54.5%) being females.

These data are from a limited number of individuals, however, as most natal females emigrated from Bossou or died between the age of 5 and 15, and there have been no new immigrant females join the group.

Changes of Demographic Parameters Over Time

Reproductive parameters are compared from recent data to previous reports published 17 and 32 years after the start of the study (Sugiyama 1994, Sugiyama & Fujita 2011; Table 1). The primiparous age of young active females born in the Bossou group has decreased since the last report, but that did not significantly change the group's reproductive parameters, perhaps because nutritional capacity in the environment changed little while the population began to decline.

DISCUSSION

Social Organization and Reproductive Success

Field primatology after World War II began with research on Japanese macaques (*Macaca fuscata*) in early 1950s, focusing on social organization and social behavior (Itani 1953, 1985). Chimpanzee studies began in early 1960s focusing mainly on social and cultural behaviors (Goodall 1963). Thereafter, many studies on nonhuman primates focused more on special characteristics of primates. For example, adaptation to the environment leads to healthier (and more) offspring and the species' social and cultural behaviors are parts of this process. To better predict the success of a species, the study of reproductive success is important for the individual and the preservation of individual populations.

In many primate species, group members of one or both sexes transfer from their natal group as adolescents or young adults. As such, studies of the long-term reproductive success of great apes are few (Bronikowski *et al.* 2016). Ours is one of the few studies to calculate the long-term reproductive success of a group of chimpanzees from the perspective of both males and females; most previous studies of reproductive parameters have focused only on females (Wallis 1997).

The most serious problem for Bossou chimpanzees is their imminent extinction, despite

Table 1. The main reproductive parameters of chimpanzees at Bossou.

Year/time since the beginning of data collection	Age at first birth (range)	Interbirth interval (range) *	Individual lifetime reproductive output (average no. of infants)	References
1993/ 17yrs	13 (12-14)	5.1 (3-11)	6.5	Sugiyama, 1994
2003/ 28 yrs	10.6 (9.5-13)	5.2		Sugiyama & Fujita 2011
2025/ 50 yrs	11.4 (8-14)	5.5 (3-11)	5.23	This study

* omitted infant death less than 5 years old

the high reproductive success of individual females over the last 50 years. Some of the females who disappeared may be living outside of Bossou and continue to reproduce, but we have no way to verify this. Thus, while the population was showing healthy levels of reproductive success the actual population size decreased. It seems to be only a matter of time before the Bossou population goes extinct

Reproductive Opportunity of Emigrant Females and the Absence of Female Immigration at Bossou

According to all previous studies on wild chimpanzees, all or most females emigrate from their natal groups and immigrate to adjacent groups as adolescents or young adults (e.g., Goodall 1986; Nishida 2012; Nakamura *et al.* 2016; this study). Recruitment of reproductive females from outside and outbreeding by natal females is necessary for

the long survival of chimpanzee populations. This begs the question as to why no female immigration occurred in Bossou.

Males that Disappeared, and Their Reproductive Opportunity

While most published reports focus on female chimpanzee reproductive opportunity, no one has discussed the reproductive future of young males who may have emigrated, because male disappearances are often automatically considered to be due to the death of the individual (Nakamura 2016; Sugiyama 2022).

In all chimpanzee groups ever studied in their natural environment, there were more adult females than adult males. Though some males remain in their natal group, others have disappeared (e.g., Muller & Wrangham 2014), for no apparent reason or signs of illness. At Bossou, a few males remained

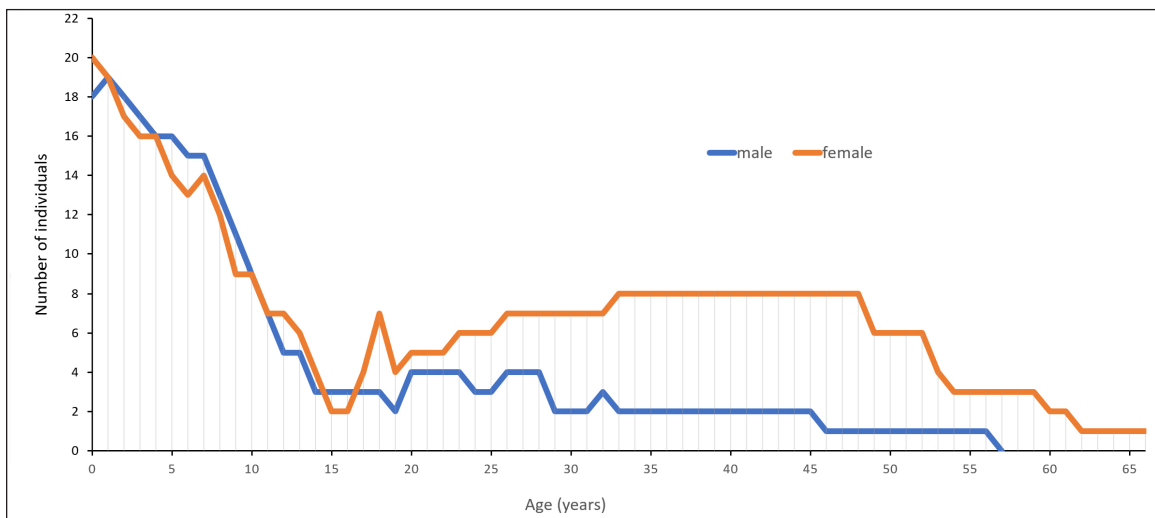


Figure 4. Number of individuals of each age/sex in the Bossou chimpanzee group through 50 years, 1976-2025. The increase of females of 18 or more years depends on adults who were in the group since the beginning of the study. The figure shows most of the males and females disappeared before reaching 16-17 years of age. After 18 years of age, members were almost stable until their deaths because there was no immigration into the group.

in their natal group, but many more disappeared. There was no sex difference in the disappearing rate of 5-15-year-olds, the species' most active and adventurous age groups (Muller & Wrangham 2014; Bronikowski *et al.* 2016). At least some of these males might have emigrated voluntarily to search for more resources, avoid mating with relatives, or find greater mating access opportunities (Figure 4).

At present, a better understanding of the fate of males that disappear must be given higher priority in chimpanzee studies. We need to know if they had any opportunity to sire offspring in their natal group and/or in another group they may have joined later. At least in Bossou we have DNA evidence of one infant that did not match the genetic profile of any of the resident males and, therefore, must have been sired by an extra-group male (Sugiyama *et al.* 1993; McCarthy *et al.* 2018). Bossou females sometimes travel separately from their group and may be mating with such extra-group males though we have no direct observation of such matings.

Many primate species have one-male and multi-female groups, e.g., Hanuman langurs (*Presbytis entellus*) (Sugiyama 1963). In these examples many males stay alone or form all-male parties outside of the reproductive group. They try to mate with group females, sometimes by taking over a group of females and other times approaching the periphery of a group. Some of these males may succeed to sire infants at least once in their long lifetime (Sugiyama 1984).

But what about chimpanzees? Although it is hard to document, male reproductive opportunity is important for understanding chimpanzee social structure. To the best of our knowledge, there are no detailed observations of males after they have left their natal group.

Over-habituation

As this study suggests, the population size of the Bossou chimpanzee group remained stable, at approximately 20 individuals, between 1976 (perhaps from as early as the 1960s, Kortlandt 1962) until 2002. Therefore, we predict that carrying capacity of the forest of Bossou is around 20 chimpanzees, with no dramatic changes in forest size and composition until 2002 according to our observations. Data suggests that the forest temporarily expanded between the 1960s to 1970s (Yamakoshi & Leblan 2013). The lack of female immigration must be one of the main reasons the population size decreased. The human population increased from 1990-2000s with

the influx of refugees from neighboring countries may have played a role (see Figure 4) (Sugiyama 2008). From our observation and villagers' accounts, human inhabitants and cultivated fields slightly increased but the main part of the chimpanzee range and villagers' attitude to chimpanzees did not change until about the early 2000s. Change occurred in the attitude of some visiting researchers, as well. Despite existing rules regarding maintaining a safe distance, they approached close to the chimpanzees for better observation. The researchers became more comfortable being close to chimpanzees and the chimpanzees habituated to having humans – both researchers and villagers – in proximity. This led to over-habituation.

A remarkable change of the Bossou chimpanzees' behavior after 2000-2010 can be seen as follows. Chimpanzees, mostly males, came into the village gardens and climbed up papaya trees to take fruits, a behavior that we had never seen before 2010. Chimpanzees sometimes approached researchers within 5m when they were looking the other way, even while on the ground. This was a behavior that was rarely seen before. Males accepted researchers within 7-10 m on the ground which was rarely seen before 2010 too. Sometimes males, adults and adolescents, attacked women and children when they were carrying bananas or other fruits from the fields to the village. This was also never seen before 2010. We were now aware of a troubling change in the villager-chimpanzee relationship possibly caused by the researchers' behavior.

Extinction of a Local Population

Why have no females immigrated to the Bossou population? We speculate there are three possible hypotheses.

The first hypothesis could be that the group's over-habituation to humans makes it difficult for unhabituated, more human-shy, females from other groups to approach the Bossou group. Out-group female chimpanzees may be avoiding the Bossou group because of the proximity maintained between chimpanzees and humans, mainly researchers, spending long hours with them in the forest.

The second hypothesis is that although adjacent groups are only 6 km away, they are separated by savanna, cultivated fields, villages, and roads. The home range of chimpanzees is fragmented into several parts by a road and lanes which have gradually broadened since about 2000. Risk-averse chimpanzees, particularly lone females or those with

young offspring, avoid traversing such areas. Even Bossou females avoid going into cultivation fields and crossing roads alone.

The third hypothesis is the loud music and vocalization uttered by villagers, especially on the days of market, festivals, and other meetings – as well as increasing traffic noise. Market and traffic noise have increased greatly since around 2000. However, if such noises were the reason for strangers' avoidance, it may be that all seven adult female chimpanzees who were in Bossou since the start of the research were not immigrants. We had no information on the general environment before we began the study to know whether these circumstances were similar then or not. Were all these females born in Bossou? It is difficult to expect so considering immigration trends reported by other researchers (Goodall 1986; Nakamura 2016).

The first mentioned hypothesis for lack of immigrants is supported as there were two (male) immigrants in the very early stages of the study, but not later. Over-habituation caused by researchers, not by villagers, may have kept shy chimpanzees from adjacent populations away. The weak point of this hypothesis is that in the other research sites chimpanzee transfers are common even when they are more habituated than at Bossou (Goodall 1963). The second hypothesis is supported by our observation that Bossou females were very shy to come out to open field. The weak point of this hypothesis is that the original seven females assumed to be immigrated from other sites. The third hypothesis may have worked as a barrier against shy females too, at least in more recent years.

In the end, no one thing can be confirmed as the sole cause of the lack of immigration to Bossou during the study period; all described factors likely played a role over time.

This study presented the reproductive parameters and discussed the unique situation of the Bossou chimpanzee populations. Comparative discussion, including data on chimpanzees at other sites and related species, will be done in a future article as that is a more complex subject.

Finally, our research team must stop the daily tracking of chimpanzees in Bossou which has been discontinued since 1976. While our research activities have terminated, we are periodically sending a few individuals to Bossou for short periods to monitor any changes of the situation. We will see if chimpanzees eventually come from other habitats to join the remaining group. We do not expect chimpanzees will be artificially introduced from other wild populations or captive ones as

these actions would disturb the natural ecosystem. Chimpanzee research and conservation at Bossou and Nimba continues under local research authority.

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