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Female chimpanzees giving first birth in their natal group in Mahale: Attention to incest between brothers and sisters

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This study was purely observational and noninvasive. Permission to study wild chimpanzees in Mahale Mountains National Park was granted by the Tanzanian Commission for Science and Technology, the Tanzanian Wildlife Research Institute, and Tanzania National Parks (permit numbers 2010-215-NA-2009-26, 2011-166-ER-2006-26, 2012-409-ER-2009-26, 2014-23-NA-2005-40, and 2015-165-ER-2009-26). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

Author contributions:

All authors contributed to the conception and design of the study. Behavioral data collection was performed by TM, SH, and TK. DNA analysis and material preparation were performed by TM, TH, and EI. The first draft of the manuscript was prepared by TM and all authors revised the manuscript. All authors read and approved the final manuscript.

Abstract

Chimpanzee societies generally show male philopatry and female dispersal. However, demographic data on wild chimpanzee societies from long-term study sites have revealed that some females give birth in their natal group (i.e., “remaining females”). Here, we report two remaining females in the M group in Mahale, Tanzania, and compare their cases with previous reports to explore the social and ecological factors that lead to females remaining in their natal group. The results showed that neither the social traits of the remaining females nor the ecological factors they experienced showed a coherent trend. However, we found multiple, non-mutually exclusive potential factors that may influence the decision of females to remain in their natal group: a decrease in indirect feeding competition, support from mothers or allomothers in the care of offspring and in aggressive interactions with other individuals, close relationships with the other remaining females, and a short adolescent infertility period. Additionally, we observed a natal female copulating with her older brother, which was the first observation of brother–sister incest in Mahale. Although DNA analysis revealed that her infant was not a product of inbreeding, the pair copulated frequently in the latter half of her estrus period, suggesting that they did not avoid incest behaviorally to avoid inbreeding. Furthermore, there was no hard evidence that the remaining female avoided mating with her maternal brother, suggesting that incest avoidance may not be a proximate factor responsible for female dispersal.

Keywords Female dispersal pattern**,** Adolescent infertility**,** Incest breeding, Social structure, Paternity identification

Introduction

Among most mammalian species that form groups with stable membership, individuals of either sex or both sexes will migrate to other groups. Previous research has revealed and emphasized sex-related differences in the dispersal patterns of mammals by comparing the advantages (avoidance of incestuous breeding, avoidance of feeding competition with relatives, and opportunity to transfer to a better group in terms of natural resources and sexual mates) and disadvantages (end of support from relatives, lack of familiarity with new group surroundings, aggressive behavior by members of the new group, and delay of breeding) of natal dispersal between the two sexes (Bonte et al. 2012; Clutton-Brock 1989; Clutton-Brock and Lukas 2012).

Previous studies have showed that, among some primate species that are characterized as being female-dispersing, some females do not transfer to other groups and instead gave birth to their first offspring in their natal group (e.g., spider monkey [*Ateles sp.*] [G. Ramos-Fernández, personal communication in Shimooka et al. 2008], red howler monkey [*Alouatta seniculus*] [Crockett and Pope 1993], and numerous cases in the chimpanzee [*Pan troglodytes*]) (Table 1). Although it is important to understand natal dispersal in terms of sex differences, it is also essential to focus on individual or local differences between female primates, with regard to natal dispersal. From this perspective, chimpanzees are the most appropriate species to investigate the ecological and social factors that affect the decision making of female primates with regard to social dispersal, because there is a large amount of demographic and behavioral data on wild chimpanzees from multiple long-term study sites.

[INSERT TABLE 1 HERE]

Demographic data on wild chimpanzees in long-term study sites have revealed that most female chimpanzees emigrate from their natal groups at puberty (Nishida et al. 2003), whereas most male chimpanzees remain in their natal groups, although Sugiyama and Fujita (2011) reported possible cases of migration of two males in Bossou, Republic of Guinea. These sex differences in the social distribution pattern are consistent with the spatial distribution pattern of chimpanzees shown by genetic analyses (Morin et al. 1994). However, data from long-term study sites have shown that females sometimes do not emigrate and instead give birth in their natal groups; these females are called “remaining females” in this study. There are differences among study groups in the rates of remaining females (Table 1).

Female chimpanzees emigrate to avoid incest and decrease deleterious genetic effects in the offspring (Pusey and Wolf 1996). On the other hand, previous studies reported cases in which remaining females received support from female relatives in their natal group (Nakamura and Hosaka 2015; Sakamaki et al. 2001; Wroblewski 2008). Another reason for female emigration is the avoidance of indirect feeding competition in the natal group (Pusey 1978). However, familiarity with and ease of access to local feeding sites may be an advantage for females to remain in their natal group. Because remaining females are likely to know the locations of feeding patches in the ranging areas of their natal groups and, therefore, need not establish new core areas for feeding, they may presumably be able to feed more efficiently than females that have immigrated from another group (Nishida et al. 2003; Pusey 1978). Additionally, as immigrant females increase feeding competition for resident females (Pusey 1978), the latter are known to show aggressive behavior to immigrant females, especially to recent immigrants (Hayakawa et al. 2011; Kahlenberg et al. 2008a, b; Nishida 1989; Nishida et al. 2003; Pusey 1980); but see also Hanamura (2015) for contradictory observations, i.e., support to immigrants by resident females in agonistic interactions. Remaining females, however, may not be subject to such aggressive behavior because they have already established their core areas (Nishida et al. 2003).

If the advantages of remaining in their natal group exceed the disadvantages, female chimpanzees may choose to give birth in their natal groups. However, data on remaining females are limited and mostly derived from the Kasakela group in Gombe, where the rate of remaining females is particularly high (Table 1). This high rate of remaining females in the Kasakela group may be due to the fact that they had only two neighboring groups as options for emigration (Nishida 2012), which is supported by the fact that chimpanzees in the three groups were genetically isolated from other chimpanzee habitats (Morin et al. 1994). Therefore, to explain why female chimpanzees emigrate from or remain in their natal groups, it is necessary to obtain data on remaining females that have many neighboring groups as options for emigration.

In Mahale, there were estimated to be four neighboring groups near the M group (Sakamaki and Nakamura 2015), and gene flow to other chimpanzee habitats was confirmed (Inoue 2015; Inoue et al. 2013). The principal aim of this study was to provide a detailed report of the two recent cases of remaining females and to discuss the factors influencing their decision to remain. We compared the social and ecological traits of these two cases of remaining females to those of five previously reported cases in Mahale to explore common traits. Specifically, we determined mating behaviors, support from female relatives, and the demography of the M group before and after the sexual maturity of the two females (as an indirect indicator for evaluating the degree of feeding competition). Additionally, we determined the paternity of the offspring of the remaining female who had incestuous encounters and explored whether incest avoidance may be a factor affecting female dispersal.

Methods

This study was conducted in Mahale Mountains National Park, Tanzania (see Nakamura and Itoh [2015] for detailed information). The eastern chimpanzees (*Pan troglodytes schweinfurthii*) of the M group have been studied since 1965, and the members of the group were almost fully identified in 1980 (Hiraiwa-Hasegawa et al. 1984). The study subjects were two female chimpanzees who were born and had given birth to their first offspring in the M group (their natal group). They are referred to as "remaining females" in this study.

One of the remaining females was Puffy (PF), born in April 2000 (Figure 1). Her first offspring was first observed on May 20, 2014 when PF was 14 years and 1 month old. The last observation of PF prior to the birth of her baby was on April 19, 2014. She had one sexually mature maternal brother, Primus (PR), born in May 1991, who was the alpha male of the M group during the behavioral observation period in this study. Pinky (PI), the mother of PF and PR, had immigrated from another group (Nakamura and Hosaka 2015) and died in 2006 when PF was 6 years old (Hanamura et al. 2008). After the death of PI, a nonrelative female, Gwekulo (GW), who reportedly had a close relationship with PI, cared for PF. Therefore, GW can be regarded as the allomother of PF (Nakamura and Hosaka 2015; MMCRP record).

The second remaining female was Xantip (XP), born in November 2000 (Figure 2). Her first offspring was first observed on November 15, 2012 when XP was 12 years and 0 months old. The last observation of XP prior to the birth of her baby was on November 2, 2012. Christmas (XM), born in April 1995, was a sexually mature maternal brother of XP, and his rank in the group was not apparently high during the behavioral observation period. Christina (XT), the mother of XP and XM, had immigrated from another group (Nakamura and Hosaka 2015; MMCRP record) and was still alive at the end of the study period.

[INSERT FIGURE 1 HERE]

[INSERT FIGURE 2 HERE]

We added the data obtained in the present study to data obtained from the literature to evaluate the possible factors influencing female chimpanzees to remain in their natal group. To determine the frequency of remaining females, using demographic data obtained from Nakamura (2015) and from this study, we divided female chimpanzees who were born in the M group between 1980 and 2003 and reached 9 years of age (i.e., the possible age of emigration) into three groups at 8-year intervals. We classified females born in 1980–1987, 1988–1995, and 1996–2003 into periods I, II, and III, respectively, and excluded two females who were presumed dead from the analysis. We used nonparametric statistics to compare the rates of remaining females between these periods, using a two-tailed Fisher's exact test in R version 3.6.3 (R Core Team, 2020).

Behavioral observations were conducted intermittently from May 2012 to October 2014, using ad libitum sampling. For incestuous behaviors, we recorded the names of males who mated or attempted to mate with females and detailed mating behaviors, including the males' possessive behaviors (Hasegawa and Hiraiwa-Hasegawa 1983; Tutin 1979) and shrub-bending behaviors—often used in the context of courtship in Mahale (Nishida 1997)—towards the subject females. If sperm was observed on the ground or on the genitals of the female subjects or male mates, we regarded the mating as "with ejaculation." If a female drew away from a male showing courtship behavior and/or trying to mount her (e.g., pulled herself forward when a male put his hands on her waist), we regarded the behavior as "refusing." Additionally, we recorded the daily attendance of the individuals, any births that took place, and the occurrence of estrus in the females.

Fecal samples from PF's infant were collected and preserved in lysis buffer (0.5 % sodium dodecyl sulfate, 100 mM ethylenediaminetetraacetic acid, 100 mM Tris-

HCl, and 10 mM NaCl) (Longmire et al. 1997) until DNA extraction. The genotypes of 54 individuals, including PF, have previously been reported (Inoue et al. 2008). We determined the genotypes of PF's offspring following the protocols of Inoue et al. (2008), with minor modifications. Multiplex polymerase chain reaction (PCR) was conducted with two primer sets: set 1 (D9s910, D11s2002, D2s1329, D7s817) and set 2 (D12s66, D2s1326, D5s1470, D7s2204). We set two and three PCR replicates for determining heterozygous and homozygous loci, respectively (Lampa et al. 2013).

Parentage analysis of PF's infant was conducted using CERVUS software (Marshall et al. 1998). We included previously genotyped individuals for paternity analysis. We had genotypes of 13 males among 15 paternal candidates for PF's offspring.

Results

Of the 13 females that were born in the M group during period I (1980–1987), 5 females remained in their natal group; of the 3 females that were born during period II (1988–1995), no females remained in their natal group; and of the 14 females that were born during period III (1996–2003), 2 females remained in their natal group. No significant differences were detected among these periods in the rate of remaining females ($P > 0.1$, Fisher's exact test, two-tailed).

In total, there were 7 remaining females out of 30 females born, including one female (Tula) who was presumed to have emigrated after the death of her first offspring (Nakamura 2015; MMCRP record). The 5 remaining females in period I experienced a drastic decrease in their natal group size between 1984 (102 individuals) and 1997 (46 individuals), when they had grown to adolescence (see Table 2 for their birth years) (Nishida et al. 2003). In contrast, the size of the M group did not change substantially and stayed at approximately 60 individuals after 2000 when the two remaining females in period III, the focal subjects of this study, were born (Nakamura 2015; MMCRP record).

[INSERT TABLE 2 HERE]

Table 2 shows the reproductive life history of the remaining females and the presence or absence of their mothers and older brothers (relatives who may give support to remaining females) when they gave birth for the first time. We could not find a definite connection between the presence of mothers or older brothers and the first birth of the females who remained in their natal group; however, the sample size was small. We observed that the mother and allomother took care of (played with or groomed) the offspring of the two remaining females. We also observed one case in which the allomother (GW) of PF supported her during minor aggressive interactions with other individuals, although there was no notable support from the mother (XT) given to the other remaining female (XP) during aggressive interactions with other individuals.

On January 7, 2013, we observed incest between PF and her maternal brother (PR) for the first time. PR groomed PF, and when PF changed her posture, PR moved to a mounting position on PF and thrust slowly, three times, without ejaculation. PF did not exhibit refusal behavior, and PR began to groom PF again after the event. PF was in estrus (showing maximum swelling) that day, and we also observed mating between PF and males other than PR.

During another estrus period of PF in which the maximum genital swelling began on March 2 to 5 and ended on March 16, 2013, we observed some sexual behaviors between PF and PR (see detailed interactions in the Supplementary Table). On March 9, we observed genital checking of PF by PR; on March 10, we observed incest with ejaculation between PF and PR for the first time. Subsequently, incest between the pair was observed on March 11, 14, and 15. Incest (four times in total) occurred during the latter half of the maximum genital swelling period. Possessive behaviors (3 days) and shrub bending (2 days) by PR towards PF were observed only during this time. After shrub bending on March 15, PF approached PR and exhibited presenting behavior towards PR. PF then showed refusing behavior to a mounting trial and courtship behaviors by PR. We observed only one adolescent female and one adult female in estrus other than PF during PF's estrus periods.

Given that the gestation period of chimpanzees is 7.5 months (Roof et al. 2005; Tutin and McGinnis 1981; Wallis 1997), we presumed that PF had conceived her offspring during September or October 2013. Although maximum genital swelling was recorded, no mating behavior by PF was observed for at least three observation days during this period.

We compared the genotypes of PR, PF, and her infant (Table 3). PR had mismatches at three loci among PR-PF-PF's infant trio. CERVUS assigned Darwin, an adult male in the M group, as the father of PF's infant, with a 99% confidence level.

[INSERT TABLE 3 HERE]

In contrast, we did not observe incest between XP and her brother XM, at least in our fragmentary ad libitum observations. Ten pairs of brothers and sisters had coresided after sexual maturity (after 9 years of age) in the Mahale M group since 1980 (Table 4). We examined the differences in coresiding period, age, and age at maternal death as possible factors related to the occurrence or nonoccurrence of incest between the PF–PR pair and the other nine pairs. We did not find a cohesive tendency that explained the difference in the occurrence or nonoccurrence of incest among the pairs. Although male ranking had not been reported consistently through the decades, reliable data had been accumulated on alpha males (e.g., Hosaka 2015), which revealed that only PR had alpha male status during the time that his sister (PF) resided in the M group.

[INSERT TABLE 4 HERE]

Discussion

In the present study, the rate of remaining females born in period I was higher than that of remaining females born in period III, although there were no significant differences in the total numbers of remaining and emigrated females between periods I, II, and III. The reduction in group size that was observed during period I resulted in a decrease in competition for food and may have been a major factor influencing the five females to remain in their natal group during this period (Nishida et al. 2003). The two remaining females born in period III would not have experienced an obvious decrease in group size and the associated reduction in feeding competition. However, the following two factors may indicate that they experienced a reduction in feeding competition: the availability of *Saba comorensis* fruit, which is one of the most important food sources for chimpanzees in Mahale (Itoh 2004; Itoh and Nishida 2007), has increased since 1996 (Itoh and Nakamura 2015); and more females than usual had immigrated to M group in

2010 (Hayakawa et al. 2011), indirectly demonstrating the abundance of food sources in their range. Therefore, it can be inferred that the increased availability of food and the consequent reduction in the competition for food may be the major reason why PF and XP remained with their natal group. A reduction in feeding competition may be one of the factors affecting the decision of female chimpanzees to remain in or emigrate from their natal groups; however, more data on food availability are required to validate this claim.

Daily support from the mother (or allomother), such as assistance in the care of offspring, which PF and XP received, and support in aggressive interactions with other individuals may be the reasons that PF and XP chose to remain in their natal group. Previous studies reported that a remaining female, RB, tended to neglect one of her offspring, and the care provided by RB’s mother was essential for the survival of the offspring (Nakamura and Hosaka 2015). RB’s mother even tried to intervene in an infanticide of the offspring of the remaining female (i.e., her grandchild) by male members of the group (Sakamaki et al. 2001). These cases suggest that the daily support and help in emergencies from the mother (or allomother) may be important for infants of remaining females and may be a reason why some females remain in their natal groups (Nakamura and Hosaka 2015; Wroblewski 2008).

Individuals of similar age may represent attractive social partners because they have had more opportunities to interact with each other in their younger days and, as a result, have developed a close relationship that may continue into adolescence and adulthood (cf. Mitani et al. 2002a). For example, male chimpanzees preferentially form coalitions and share meat with individuals of similar age (Mitani et al. 2002b). The two remaining females in this study, PF and XP, were similar in age. There is evidence suggesting a close relationship between the two females: they were caregivers of the same infant (an offspring of XP's mother who was born in 2008) at the same time (Nakamura and Hosaka 2015). Four of five previously reported remaining females (TL, AK, AB, and TZ) were also similar in age (Table 2) and were presumed to maintain strong associations. In fact, two of them, TZ and AK, were reported to form a particularly close relationship (Nishida 2008). Additionally, in a 1-year study conducted in 2005 and 2006 using focal animal sampling, AK's rate of dyadic association (i.e., spending time together in the same party) with TZ and AB was around three and two times higher (14.7% and 8.6%, respectively) than her average association rate with other females (5.5%) (Hanamura, unpublished data), although in this period they were well past the age of adolescence during which most female chimpanzees emigrate from their natal groups. Therefore, six of the seven remaining females in Mahale had other remaining females of similar age with whom they presumably had a high association. Although some females who had similar-aged conspecifics in the natal group emigrated, these results suggest that the decision of females to remain in a natal group or emigrate may be linked to the decision of other females with whom they have close relationships. If this is correct, and as the play among immature chimpanzees changes in "fashion" (Matsusaka et al. 2006), female decision making regarding social dispersal may also be considered a "fashion." Although previous studies have focused on ecological (e.g., feeding competition) and genetic (e.g., incest) factors affecting the decision of females to remain in or emigrate from their natal groups, these social factors should also be considered.

XP was expected to have conceived her first offspring at 11.4 years of age, which coincides with the age when other females born in the M group typically emigrated (median 11.00, mean 11.24 ± 1.30 SD, n = 41) (Nakamura 2015). Given that female chimpanzees usually continue to stay in the group in which they give birth to their first offspring (Matsumoto and Hayaki 2015), XP's decision to remain in her natal M group may have been due to a short "adolescent infertility" period (Nishida et al. 2003), that is, early conception and giving birth before the usual age of emigration. One of the five previous remaining females in the M group, RB, may be a similar case (cf. Nakamura 2015).

The two remaining females in this study, born in 2000, were reported a long time after the last remaining female, born in 1986 (Nakamura 2015). This may give the impression that female chimpanzees rarely give birth in their natal group. However, one of the major reasons for this is that females reaching 9 years of age (i.e., the eligible age for emigration) were few in the intermedial period (13, 3, and 14 females born between 1980 and 1987, 1988 and 1995, and 1996 and 2003, respectively). There were no significant differences among the periods in the rate of remaining females. Given this fact, and considering that remaining females have been reported in the majority of chimpanzee groups that have been the subject of long-term studies (Table 1), we suggest that the “remaining female” phenomenon is not an exception, but rather a common occurrence in chimpanzee societies. Therefore, female chimpanzees can always choose to give birth to their first offspring in their natal group, depending on conditions we have discussed here.

There are no reports of offspring of females and their maternal brothers in chimpanzees (Constable et al. 2001; Inoue et al. 2008). We observed mating and courtship behaviors between PF and PR occurring in the latter half of the estrus period, when ovulation tends to occur (Deschner et al. 2003). However, DNA analysis showed that it was highly unlikely that PR was the father of PF’s offspring. These results suggest that

PF and PR did not avoid incest behaviorally (i.e., they did not avoid mating when PF was ovulating) in order to avoid inbreeding (genetic incest).

Close relationships before sexual maturity most likely contribute to incest avoidance among primate species, including chimpanzees (Pusey 1978, 1980). In chimpanzees, a maternal sister and brother who are close in age may form an intimate relationship because they often travel in the same party with their mother. PF and PR may have had fewer interactions than other sister–brother pairs of similar age whose mothers were still alive because of the 9-year difference in age between them; additionally, their mother died when PF was 6 years old (Nakamura and Hosaka 2015). However, the case of PF and PR was not an isolated one with regard to the age gap and the presence of a living mother (Table 4). Given that PR was the only alpha male among the coresiding male relatives of the seven remaining females in the Mahale M group, it is possible that male harassment contributed to incest, although females could sometimes refuse to mate with or be courted by alpha males. We observed that PF sometimes refused to mate with or be courted by her brother. However, it is unclear whether PF refused because of the insistent courtship and attempted mating by the alpha male (females also react in this way to unrelated males in similar circumstances) or a desire to avoid mating with her brother. In summary, we did not find any behavioral evidence that PF avoided mating with her maternal brother. Goodall (1986) also reported that some females in Gombe did not seem to reject incest (or trial mating) with their brothers, whereas others did. These results agree with those of Stumpf et al. (2009), which suggested that inbreeding avoidance is not a proximate factor determining female dispersal in chimpanzees.

In conclusion, this study suggests that the phenomenon of females remaining in their natal group is not an exception in chimpanzee societies and that there are several non-mutually exclusive factors that influence the decision of females to remain in their natal groups. These factors include decreased indirect feeding competition resulting from a decrease in group size and/or an increase in environmental carrying capacity, support from mothers or allomothers in the care of offspring and in aggressive interactions with other individuals, close relationships with other remaining females of a similar age in the group, and short adolescent infertility periods. Incest avoidance may not be a proximate factor responsible for female dispersal. Long-term research at multiple chimpanzee field sites and accumulation of detailed case studies on remaining females may help to draw valid conclusions about female social dispersal patterns in chimpanzee societies and gain a better understanding of the detailed behavioral aspects of natal dispersal in animals.

Disclosure of potential conflicts of interest

The authors declare that they have no conflicts of interest.

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Figure Legends

Figure 1. Remaining female Puffy (PF) (right), carrying her infant

Figure 2. Remaining female Xantip (XP) (middle), her infant (left), and her mother Christina (XT) (right)

Figure 1

Figure 2

Table 1 Remaining females of wild chimpanzees at long-term research sites

Site	Group	Species	Number of remaining females[1]	Source
Mahale, Tanzania	M	*Pan troglodytes schweinfurthii*	7 of 30 (23.3%)[2]	Nishida et al. 2003; Nakamura. 2015; this study
Gombe, Tanzania	Kasakela	*P. t. schweinfurthii*	6 of 11 (54.5%)[3]	Pusey et al. 1997
	Kasakela and Mitumba	*P. t. schweinfurthii*	12 of 24 (50.0%)	Walker et al. 2018
Kibale, Uganda	Kanyawara	*P. t. schweinfurthii*	1 of 9 (11.1%)	Stumpf et al. 2009
Taï, Côte d'Ivoire	North	*P. t. verus*	3 of 17 (17.6%)	Boesch and Boesch-Achermann 2000; Wittig and Boesch 2019
	South	*P. t. verus*	1 of 12 (8.3%)	Wittig and Boesch 2019
Bossou, Guinea	Bossou	*P. t. verus*	5 of 8 (62.5%)	Sugiyama et al. 1999; 2004; Sugiyama and Fujita 2011

[1] Shows the number of females who first gave birth in their natal group (i.e., the remaining females) out of the total number of remaining females and nulliparous females who were estimated to emigrate.
[2] One remaining female was estimated to emigrate to another group after the death of her first offspring.
[3] "6 settled as adults in the community, 5 transferred to other communities, and 3 disappeared" (Pusey et al. 1997).

Table 2 Birth year and year of first reproduction, living mothers and older brothers at the first reproduction, and observed incest of remaining females in the M group

Name	**Abbreviation**	**Birth period**	**Birth year**	**First reproduction**	**Mother living**	**Older brother living**	**Reference**
Tula	TL[1]	I	1980	1993	No	Yes	Nakamura, 2015
Ako	AK[2]	I	1981	1995	No	No	Nakamura, 2015
Abi	AB	I	1982	1998	No	Yes	Nakamura, 2015
Totzy	TZ	I	1982	1995	Yes	No	Nakamura, 2015
Ruby	RB	I	1986	1998	Yes	No	Nakamura, 2015
Puffy	PF	III	2000	2014	No[3]	Yes	This study; Nakamura, 2015
Xantip	XP	III	2000	2012	Yes	Yes	This study; Nakamura, 2015

[1] TL emigrated to the B group after the death of her first offspring.

[2] AK was thought to be born in the M group.

[3] PF's allomother, Gwekulo (GW), was alive.

Table 3 Genotypes at eight microsatellite loci of a remaining female, Puffy, her brother, Primus, her offspring, and a candidate father of the infant, Darwin. Primus had mismatches at D2s1329, D12s66, and D7s817

Name	**D9s910**	**D11s2002**	**D2s1329**	**D12s66**	**D2s1326**	**D5s1470**	**D7s2204**	**D7s817**	**Reference**
Primus (PR)	104/110	148/148	178/198	150/150	206/206	190/190	233/253	148/148	Inoue et al. 2008
Darwin (DW)	104/110	148/148	198/202	154/158	206/206	-	249/253	144/148	Inoue et al. 2008
Puffy (PF)	104/104	144/148	186/198	158/182	206/206	190/194	233/245	124/148	Inoue et al. 2008
PF's offspring	104/104	144/148	186/202	158/158	206/206	190/190	245/253	144/148	This study

Table 4 Pairs of sisters and brothers who coresided even after they had both reached sexual maturity (i.e., 9 years of age) in the Mahale M group

Sister[1]	**Birth year**[2]	**Brother**[1]	**Incest**	**Coresiding period (mo)**	**Age difference (mo)**[2]	**Older sibling**	**Age of sister when maternal death occurred (mo)**[3]	**Reference**
Puffy (PF)	2000	Primus (PR)	Observed	>61[4]	107	Brother	74	This study; MMCRP record
Katyentye	1967?	Bembe	–	47–59	60?	Sister	Coresiding	Nishida 2012; MMCRP record
Bunde	1977?	Bembe	–	49	60?	Brother	Coresiding	Nishida 2012; MMCRP record
Wasiwasi	1978?	Shike	–	0–4	108?	Brother	Coresiding	Nishida 2012; MMCRP record
Tula (TL)	1980	Nsaba	–	54	79	Brother	76	Nishida 2012; MMCRP record
Abi (AB)	1982	Toshibo	–	46	63	Brother	88	Nishida 2012; MMCRP record
Ruby (RB)	1986	Orion	–	73	61	Sister	Coresiding	Nishida 2012; MMCRP record
Maggie	1987	Masudi	–	8	110	Brother	37	Nishida 2012; MMCRP record
Ai	1988	Alofu	–	45	80	Brother	Coresiding	Nishida 2012; MMCRP record
Xantip (XP)	2000	Christmas (XM)	–	>54[4]	67	Brother	Coresiding	This study; MMCRP record

[1] Abbreviation of the names of remaining females (i.e., first giving birth in the natal [M] group) are given in Table 3.

[2] ? indicates estimated values

[3] "Coresiding" indicates that the mother resided in the M group until both the sister and brother reached sexual maturity (i.e., 9 years of age).

[4] Values were calculated up to May 2014.

Supplementary Table 1

Sexual interactions of Puffy (PF) with her brother Primus (PR) in the period of PF's estrus during which they copulated

Date	State of PF's sexual swelling	Copulation with PR	PR's sexual behavior toward PF	Copulation with other males	Number of researchers
1 Mar 2013	No swelling	Not observed	Not observed	Not observed	1
2 Mar 2013	No data	No data	No data	No data	0
3 Mar 2013	No data	No data	No data	No data	0
4 Mar 2013	No data	No data	No data	No data	1
5 Mar 2013	Maximum swelling	Not observed	Not observed	Not observed	3
6 Mar 2013	Maximum swelling	Not observed	Not observed	Not observed	3
7 Mar 2013	Maximum swelling	Not observed	Not observed	Not observed	2
8 Mar 2013	Maximum swelling	Not observed	Not observed	2 copulations with 2 males	2
9 Mar 2013	Maximum swelling	Not observed	Genital checking	Not observed	2
10 Mar 2013	Maximum swelling	1 copulation with ejaculation	Not observed	Not observed	2
11 Mar 2013	Maximum swelling	1 copulation	Not observed	4 copulations with 4 males	3
12 Mar 2013	Maximum swelling	Not observed	Not observed	Not observed	2

13 Mar 2013	No data	No data	No data	No data	2
14 Mar 2013	Maximum swelling	1 copulation	Possessive behavior	Not observed	2
15 Mar 2013	Maximum swelling	1 copulation with ejaculation	Possessive behavior, genital checking, shrub bending	Not observed	2
16 Mar 2013	Shrinking	Not observed	Possessive behavior, shrub bending	Not observed	1

Densely shaded sections indicate no data, while lightly shaded areas indicate observed interactions

617