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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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- 1 Female chimpanzees giving first birth in their natal group in Mahale: Attention to incest
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3
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55 animals were followed.

56

57 **Author contributions:**

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

63

64 **Abstract**

65 Chimpanzee societies generally show male philopatry and female dispersal.
66 However, demographic data on wild chimpanzee societies from long-term study sites
67 have revealed that some females give birth in their natal group (i.e., “remaining females”).
68 Here, we report two remaining females in the M group in Mahale, Tanzania, and compare
69 their cases with previous reports to explore the social and ecological factors that lead to
70 females remaining in their natal group. The results showed that neither the social traits of
71 the remaining females nor the ecological factors they experienced showed a coherent
72 trend. However, we found multiple, non-mutually exclusive potential factors that may
73 influence the decision of females to remain in their natal group: a decrease in indirect
74 feeding competition, support from mothers or allomothers in the care of offspring and in

75 aggressive interactions with other individuals, close relationships with the other
76 remaining females, and a short adolescent infertility period. Additionally, we observed a
77 natal female copulating with her older brother, which was the first observation of brother–
78 sister incest in Mahale. Although DNA analysis revealed that her infant was not a product
79 of inbreeding, the pair copulated frequently in the latter half of her estrus period,
80 suggesting that they did not avoid incest behaviorally to avoid inbreeding. Furthermore,
81 there was no hard evidence that the remaining female avoided mating with her maternal
82 brother, suggesting that incest avoidance may not be a proximate factor responsible for
83 female dispersal.

84

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

87

88 **Introduction**

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

98 Previous studies have showed that, among some primate species that are
99 characterized as being female-dispersing, some females do not transfer to other groups
100 and instead gave birth to their first offspring in their natal group (e.g., spider monkey
101 [*Ateles sp.*] [G. Ramos-Fernández, personal communication in Shimooka et al. 2008], red
102 howler monkey [*Alouatta seniculus*] [Crockett and Pope 1993], and numerous cases in
103 the chimpanzee [*Pan troglodytes*]) (Table 1). Although it is important to understand natal
104 dispersal in terms of sex differences, it is also essential to focus on individual or local
105 differences between female primates, with regard to natal dispersal. From this perspective,

106 chimpanzees are the most appropriate species to investigate the ecological and social
107 factors that affect the decision making of female primates with regard to social dispersal,
108 because there is a large amount of demographic and behavioral data on wild chimpanzees
109 from multiple long-term study sites.

110 [INSERT TABLE 1 HERE]

111 Demographic data on wild chimpanzees in long-term study sites have revealed
112 that most female chimpanzees emigrate from their natal groups at puberty (Nishida et al.
113 2003), whereas most male chimpanzees remain in their natal groups, although Sugiyama
114 and Fujita (2011) reported possible cases of migration of two males in Bossou, Republic
115 of Guinea. These sex differences in the social distribution pattern are consistent with the
116 spatial distribution pattern of chimpanzees shown by genetic analyses (Morin et al. 1994).
117 However, data from long-term study sites have shown that females sometimes do not
118 emigrate and instead give birth in their natal groups; these females are called “remaining
119 females” in this study. There are differences among study groups in the rates of remaining
120 females (Table 1).

121 Female chimpanzees emigrate to avoid incest and decrease deleterious genetic
122 effects in the offspring (Pusey and Wolf 1996). On the other hand, previous studies
123 reported cases in which remaining females received support from female relatives in their

124 natal group (Nakamura and Hosaka 2015; Sakamaki et al. 2001; Wroblewski 2008).
125 Another reason for female emigration is the avoidance of indirect feeding competition in
126 the natal group (Pusey 1978). However, familiarity with and ease of access to local
127 feeding sites may be an advantage for females to remain in their natal group. Because
128 remaining females are likely to know the locations of feeding patches in the ranging areas
129 of their natal groups and, therefore, need not establish new core areas for feeding, they
130 may presumably be able to feed more efficiently than females that have immigrated from
131 another group (Nishida et al. 2003; Pusey 1978). Additionally, as immigrant females
132 increase feeding competition for resident females (Pusey 1978), the latter are known to
133 show aggressive behavior to immigrant females, especially to recent immigrants
134 (Hayakawa et al. 2011; Kahlenberg et al. 2008a, b; Nishida 1989; Nishida et al. 2003;
135 Pusey 1980); but see also Hanamura (2015) for contradictory observations, i.e., support
136 to immigrants by resident females in agonistic interactions. Remaining females, however,
137 may not be subject to such aggressive behavior because they have already established
138 their core areas (Nishida et al. 2003).

139 If the advantages of remaining in their natal group exceed the disadvantages,
140 female chimpanzees may choose to give birth in their natal groups. However, data on
141 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

160 factor affecting female dispersal.

161

162 **Methods**

163 This study was conducted in Mahale Mountains National Park, Tanzania (see
164 Nakamura and Itoh [2015] for detailed information). The eastern chimpanzees (*Pan*
165 *troglodytes schweinfurthii*) of the M group have been studied since 1965, and the
166 members of the group were almost fully identified in 1980 (Hiraiwa-Hasegawa et al.
167 1984). The study subjects were two female chimpanzees who were born and had given
168 birth to their first offspring in the M group (their natal group). They are referred to as
169 “remaining females” in this study.

170 One of the remaining females was Puffy (PF), born in April 2000 (Figure 1). Her
171 first offspring was first observed on May 20, 2014 when PF was 14 years and 1 month
172 old. The last observation of PF prior to the birth of her baby was on April 19, 2014. She
173 had one sexually mature maternal brother, Primus (PR), born in May 1991, who was the
174 alpha male of the M group during the behavioral observation period in this study. Pinky
175 (PI), the mother of PF and PR, had immigrated from another group (Nakamura and
176 Hosaka 2015) and died in 2006 when PF was 6 years old (Hanamura et al. 2008). After
177 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

196 born in 1980–1987, 1988–1995, and 1996–2003 into periods I, II, and III, respectively,
197 and excluded two females who were presumed dead from the analysis. We used
198 nonparametric statistics to compare the rates of remaining females between these periods,
199 using a two-tailed Fisher’s exact test in R version 3.6.3 (R Core Team, 2020).

200 Behavioral observations were conducted intermittently from May 2012 to
201 October 2014, using ad libitum sampling. For incestuous behaviors, we recorded the
202 names of males who mated or attempted to mate with females and detailed mating
203 behaviors, including the males’ possessive behaviors (Hasegawa and Hiraiwa-Hasegawa
204 1983; Tutin 1979) and shrub-bending behaviors—often used in the context of courtship
205 in Mahale (Nishida 1997)—towards the subject females. If sperm was observed on the
206 ground or on the genitals of the female subjects or male mates, we regarded the mating
207 as “with ejaculation.” If a female drew away from a male showing courtship behavior
208 and/or trying to mount her (e.g., pulled herself forward when a male put his hands on her
209 waist), we regarded the behavior as “refusing.” Additionally, we recorded the daily
210 attendance of the individuals, any births that took place, and the occurrence of estrus in
211 the females.

212 Fecal samples from PF’s infant were collected and preserved in lysis buffer
213 (0.5 % sodium dodecyl sulfate, 100 mM ethylenediaminetetraacetic acid, 100 mM Tris-

214 HCl, and 10 mM NaCl) (Longmire et al. 1997) until DNA extraction. The genotypes of
215 54 individuals, including PF, have previously been reported (Inoue et al. 2008). We
216 determined the genotypes of PF's offspring following the protocols of Inoue et al. (2008),
217 with minor modifications. Multiplex polymerase chain reaction (PCR) was conducted
218 with two primer sets: set 1 (D9s910, D11s2002, D2s1329, D7s817) and set 2 (D12s66,
219 D2s1326, D5s1470, D7s2204). We set two and three PCR replicates for determining
220 heterozygous and homozygous loci, respectively (Lampa et al. 2013).

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

224

225 **Results**

226 Of the 13 females that were born in the M group during period I (1980–1987), 5
227 females remained in their natal group; of the 3 females that were born during period II
228 (1988–1995), no females remained in their natal group; and of the 14 females that were
229 born during period III (1996–2003), 2 females remained in their natal group. No
230 significant differences were detected among these periods in the rate of remaining females
231 ($P > 0.1$, Fisher's exact test, two-tailed).

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

240 [INSERT TABLE 2 HERE]

241 Table 2 shows the reproductive life history of the remaining females and the
242 presence or absence of their mothers and older brothers (relatives who may give support
243 to remaining females) when they gave birth for the first time. We could not find a definite
244 connection between the presence of mothers or older brothers and the first birth of the
245 females who remained in their natal group; however, the sample size was small. We
246 observed that the mother and allomother took care of (played with or groomed) the
247 offspring of the two remaining females. We also observed one case in which the
248 allomother (GW) of PF supported her during minor aggressive interactions with other

249 individuals, although there was no notable support from the mother (XT) given to the
250 other remaining female (XP) during aggressive interactions with other individuals.

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

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

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).

321 Individuals of similar age may represent attractive social partners because they
322 have had more opportunities to interact with each other in their younger days and, as a
323 result, have developed a close relationship that may continue into adolescence and
324 adulthood (cf. Mitani et al. 2002a). For example, male chimpanzees preferentially form
325 coalitions and share meat with individuals of similar age (Mitani et al. 2002b). The two
326 remaining females in this study, PF and XP, were similar in age. There is evidence
327 suggesting a close relationship between the two females: they were caregivers of the same
328 infant (an offspring of XP's mother who was born in 2008) at the same time (Nakamura
329 and Hosaka 2015). Four of five previously reported remaining females (TL, AK, AB, and
330 TZ) were also similar in age (Table 2) and were presumed to maintain strong associations.
331 In fact, two of them, TZ and AK, were reported to form a particularly close relationship
332 (Nishida 2008). Additionally, in a 1-year study conducted in 2005 and 2006 using focal
333 animal sampling, AK's rate of dyadic association (i.e., spending time together in the same
334 party) with TZ and AB was around three and two times higher (14.7% and 8.6%,
335 respectively) than her average association rate with other females (5.5%) (Hanamura,
336 unpublished data), although in this period they were well past the age of adolescence
337 during which most female chimpanzees emigrate from their natal groups. Therefore, six
338 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).

357 The two remaining females in this study, born in 2000, were reported a long time
358 after the last remaining female, born in 1986 (Nakamura 2015). This may give the
359 impression that female chimpanzees rarely give birth in their natal group. However, one
360 of the major reasons for this is that females reaching 9 years of age (i.e., the eligible age
361 for emigration) were few in the intermedial period (13, 3, and 14 females born between
362 1980 and 1987, 1988 and 1995, and 1996 and 2003, respectively). There were no
363 significant differences among the periods in the rate of remaining females. Given this fact,
364 and considering that remaining females have been reported in the majority of chimpanzee
365 groups that have been the subject of long-term studies (Table 1), we suggest that the
366 “remaining female” phenomenon is not an exception, but rather a common occurrence in
367 chimpanzee societies. Therefore, female chimpanzees can always choose to give birth to
368 their first offspring in their natal group, depending on conditions we have discussed here.

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

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

376 Close relationships before sexual maturity most likely contribute to incest
377 avoidance among primate species, including chimpanzees (Pusey 1978, 1980). In
378 chimpanzees, a maternal sister and brother who are close in age may form an intimate
379 relationship because they often travel in the same party with their mother. PF and PR may
380 have had fewer interactions than other sister–brother pairs of similar age whose mothers
381 were still alive because of the 9-year difference in age between them; additionally, their
382 mother died when PF was 6 years old (Nakamura and Hosaka 2015). However, the case
383 of PF and PR was not an isolated one with regard to the age gap and the presence of a
384 living mother (Table 4). Given that PR was the only alpha male among the coresiding
385 male relatives of the seven remaining females in the Mahale M group, it is possible that
386 male harassment contributed to incest, although females could sometimes refuse to mate
387 with or be courted by alpha males. We observed that PF sometimes refused to mate with
388 or be courted by her brother. However, it is unclear whether PF refused because of the
389 insistent courtship and attempted mating by the alpha male (females also react in this way
390 to unrelated males in similar circumstances) or a desire to avoid mating with her brother.
391 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

410 The authors declare that they have no conflicts of interest.

411

412 **References**

413 Boesch C, Boesch-Achermann H (2000) The Chimpanzees of the Tai Forest: Behavioural

414 Ecology and Evolution. Oxford University Press, Oxford

415 Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V,

416 Matthysen E, Mustin K, Saastamoinen M (2012) Costs of dispersal. Biol Rev

417 87:290–312. <https://doi.org/10.1111/j.1469-185X.2011.00201.x>

418 Clutton-Brock TH (1989) Female transfer and inbreeding avoidance in social mammals.

419 Nature 337:70–72. <https://doi.org/10.1038/337070a0>

420 Clutton-Brock TH, Lukas D (2012) The evolution of social philopatry and dispersal in

421 female mammals. Mol Ecol 21:472–492. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-294X.2011.05232.x)

422 294X.2011.05232.x

423 Constable JL, Ashley MV, Goodall J, Pusey AE (2001) Noninvasive paternity

424 assignment in Gombe chimpanzees. Mol Ecol 10:1279–1300.

425 <https://doi.org/10.1046/j.1365-294X.2001.01262.x>

426 Crockett CM, Pope TR (1993) Consequences of sex differences in dispersal for juvenile

427 red howler monkeys. In: Pereira ME, Fairbanks LA (eds) Juvenile primates: life

- 428 history, development, and behavior, University of Chicago Press, Chicago,
429 pp104–118
- 430 Deschner T, Heistermann M, Hodges K, Boesch C (2003) Timing and probability of
431 ovulation in relation to sex skin swelling in wild West African chimpanzees,
432 *Pan troglodytes versus*. Anim Behav 66:551–560.
433 <https://doi.org/10.1006/anbe.2003.2210>
- 434 Goodall J (1986) The chimpanzees of Gombe: Patterns of behavior. Belknap Press of
435 Harvard University Press, Cambridge
- 436 Hanamura S (2015) Male-female relationships: affiliative, interventional, and dominant-
437 subordinate interactions. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds)
438 Mahale Chimpanzees: 50 years of research. Cambridge University Press,
439 Cambridge, pp 410–420
- 440 Hanamura S, Kiyono M, Lukasik-Braum M, Mlengeya T, Fujimoto M, Nakamura M,
441 Nishida T (2008) Chimpanzee deaths at Mahale caused by a flu-like disease.
442 Primates 49:77–80. <https://doi.org/10.1007/s10329-007-0054-1>
- 443 Hasegawa T, Hiraiwa-Hasegawa M (1983) Opportunistic and restrictive matings among
444 wild chimpanzees in the Mahale Mountains, Tanzania. J Ethol 1:75–85.
445 <https://doi.org/10.1007/BF02347833>

- 446 Hasegawa T, Hiraiwa-Hasegawa M (1990) Sperm Competition and Mating Behavior. In:
447 Nishida T (ed) The chimpanzees of the Mahale mountains: Sexual and life
448 history strategies. Tokyo University Press, Tokyo, pp 115–132
- 449 Hayakawa T, Nakashima M, Nakamura M (2011) Immigration of a Large Number of
450 Adolescent Female Chimpanzees into the Mahale M Group. Pan Afr News 18:
451 8–10. <https://doi.org/10.5134/143527>
- 452 Hiraiwa-Hasegawa M, Hasegawa T, Nishida T (1984) Demographic study of a large-
453 sized unit-group of chimpanzees in the Mahale Mountains, Tanzania: A
454 preliminary report. Primates 25:401–413. <https://doi.org/10.1007/BF02381663>
- 455 Hosaka K (2015) Who's who. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds)
456 Mahale Chimpanzees: 50 years of research. Cambridge University Press,
457 Cambridge, pp 48–67
- 458 Inoue E (2015) Genetic studies. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds)
459 Mahale Chimpanzees: 50 years of research. Cambridge University Press,
460 Cambridge, pp 625–638
- 461 Inoue E, Inoue-Murayama M, Vigilant L, Takenaka O, Nishida T (2008) Relatedness in
462 wild chimpanzees: influence of paternity, male philopatry, and demographic
463 factors. Am J Phys Anthropol 137:256–262. <https://doi.org/10.1002/ajpa.20865>

- 464 Inoue E, Tashiro Y, Ogawa H, Inoue-Murayama M, Nishida T, Takenaka O (2013) Gene
465 Flow and Genetic Diversity of Chimpanzees in Tanzanian Habitats. *Primate*
466 *Conserv* 26:67–74. <https://doi.org/10.1896/052.026.0105>
- 467 Itoh N (2004) Plant phenology and chimpanzee fission–fusion grouping system in Mahale
468 Mountains National Park. Dissertation, Kyoto University
- 469 Itoh N, Nakamura M (2015) Mahale flora: its historical background and long-term
470 changes. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds) Mahale
471 Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge,
472 pp 150–173
- 473 Itoh N, Nishida T (2007) Chimpanzee grouping patterns and food availability in Mahale
474 Mountains National Park, Tanzania. *Primates* 48:87–96.
475 <https://doi.org/10.1007/s10329-006-0031-0>
- 476 Kahlenberg SM, Thompson ME, Muller MN, Wrangham RW (2008a) Immigration
477 costs for female chimpanzees and male protection as an immigrant
478 counterstrategy to intrasexual aggression. *Anim Behav* 76:1497–1509.
479 <https://doi.org/10.1016/j.anbehav.2008.05.029>

- 480 Kahlenberg SM, Thompson ME, Wrangham RW (2008b) Female competition over core
481 areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. Int J
482 Primatol 29:931. <https://doi.org/10.1007/s10764-008-9276-3>
- 483 Lampa S, Henle K, Klenke R, Hoehn M, Gruber B (2013) How to overcome genotyping
484 errors in non-invasive genetic mark-recapture population size estimation—A
485 review of available methods illustrated by a case study. J Wildlife Manage
486 77:1490–1511. <https://doi.org/10.1002/jwmg.604>
- 487 Longmire JL, Maltbie M, Baker RJ (1997) Use of ‘lysis buffer’ in DNA isolation and its
488 implication for museum collections. Museum of Texas Tech University, Lubbock
- 489 Marshall T, Slate J, Kruuk L, Pemberton J (1998) Statistical confidence for likelihood-
490 based paternity inference in natural populations. Mol Ecol 7:639–655.
491 <https://doi.org/10.1046/j.1365-294x.1998.00374.x>
- 492 Matsumoto T, Itoh N, Inoue S, Nakamura M (2016) An observation of a severely
493 disabled infant chimpanzee in the wild and her interactions with her mother.
494 Primates 57:3–7. <https://doi.org/10.1007/s10329-015-0499-6>
- 495 Matsumoto T, Hayaki H (2015) Development and growth: With special reference to
496 mother–infant relationships. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds)

- 497 Mahale Chimpanzees: 50 Years of Research. Cambridge University Press,
498 Cambridge, pp 313–325.
- 499 Matsusaka T, Nishie H, Shimada M, Kutsukake N, Zamma K, Nakamura M, Nishida T
500 (2006) Tool-use for drinking water by immature chimpanzees of Mahale:
501 prevalence of an unessential behavior. *Primates* 47:113–122.
502 <https://doi.org/10.1007/s10329-005-0158-4>
- 503 Mitani JC, Watts DP, Muller MN (2002a) Recent developments in the study of wild
504 chimpanzee behavior *Evol Anthropol Issues News Rev* 11:9–25.
505 <https://doi.org/10.1002/evan.10008>
- 506 Mitani JC, Watts DP, Pepper JW, Merriwether DA (2002b) Demographic and social
507 constraints on male chimpanzee behaviour. *Anim Behav* 64:727–737.
508 <https://doi.org/10.1006/anbe.2002.4014>
- 509 Morin PA, Moore JJ, Chakraborty R, Jin L, Goodall J, Woodruff DS (1994) Kin
510 selection, social structure, gene flow, and the evolution of chimpanzees.
511 *Science* 265:1193–1201. <https://doi.org/10.1126/science.7915048>
- 512 Nakamura M (2015) Demography of the M group. In: Nakamura M, Hosaka K, Itoh N,
513 Zamma K (eds) Mahale Chimpanzees: 50 Years of Research. Cambridge
514 University Press, Cambridge, pp 82–93

- 515 Nakamura M, Hosaka K (2015) Orphans and allomothering. In: Nakamura M, Hosaka K,
516 Itoh N, Zamma K (eds) Mahale Chimpanzees: 50 Years of Research. Cambridge
517 University Press, Cambridge, pp 421–432
- 518 Nakamura M, Itoh N (2015) Overview of the field site: Mahale Mountains and their
519 surroundings. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds) Mahale
520 chimpanzees. Cambridge University Press, Cambridge, pp 7–20
- 521 Nishida T (1989) Social interactions between resident and immigrant female chimpanzees.
522 In: Heltne PG, Marquardt, LA (ed) Understanding chimpanzees. Harvard
523 University Press, Cambridge, pp 68–89
- 524 Nishida T (1997) Sexual behavior of adult male chimpanzees of the Mahale Mountains
525 National Park, Tanzania. Primates 38:379–398.
526 <https://doi.org/10.1007/BF02381879>
- 527 Nishida T (2008) [Introduction of Mahale chimpanzees: Totzy]. Mahale Chimpun, 12. In
528 Japanese.
- 529 Nishida T (2012) Chimpanzees of the lakeshore: Natural history and culture at Mahale.
530 Cambridge University Press, Cambridge
- 531 Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD,
532 Itoh N, Kawanaka K, Matsumoto-Oda A et al (2003) Demography, female life

- 533 history, and reproductive profiles among the chimpanzees of Mahale. *Am J*
534 *Primatol* 59:99–121. <https://doi.org/10.1002/ajp.10068>
- 535 Pusey A, Williams J, Goodall J (1997) The influence of dominance rank on the
536 reproductive success of female chimpanzees. *Science* 277:828–831.
537 <https://doi.org/10.1126/science.277.5327.828>
- 538 Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–
539 206. [https://doi.org/10.1016/0169-5347\(96\)10028-8](https://doi.org/10.1016/0169-5347(96)10028-8)
- 540 Pusey AE (1978) The physical and social development of wild adolescent chimpanzees
541 (*Pan troglodytes schweinfurthii*). Dissertation, Stanford University
- 542 Pusey AE (1980) Inbreeding avoidance in chimpanzees. *Anim Behav* 28:543–552.
543 [https://doi.org/10.1016/S0003-3472\(80\)80063-7](https://doi.org/10.1016/S0003-3472(80)80063-7)
- 544 R Core Team (2020) R: A language and environment for statistical computing. R
545 Foundation for Statistical Computing, Vienna, Austria.
- 546 Roof KA, Hopkins WD, Izard MK, Hook M, Schapiro SJ (2005) Maternal age, parity,
547 and reproductive outcome in captive chimpanzees (*Pan troglodytes*). *Am J*
548 *Primatol* 67:199–207. <http://doi.org/10.1002/ajp.20177>
- 549 Sakamaki T, Itoh N, Nishida T (2001) An attempted within-group infanticide in wild
550 chimpanzees. *Primates* 42:359–366. <https://doi.org/10.1007/BF02629626>

- 551 Sakamaki T, Nakamura M (2015) Intergroup relationships. In: Nakamura M, Hosaka K,
552 Itoh N, Zamma K (eds) *Mahale Chimpanzees: 50 Years of Research*.
553 Cambridge University Press, Cambridge, pp 128–139.
- 554 Shimooka Y et al. (2008) Demography and group composition of *Ateles*. In: Campbell CJ
555 (ed) *Spider monkeys: Behavior, ecology and evolution of the genus Ateles*.
556 Cambridge University Press, Cambridge, pp 329–348
- 557 Stumpf R, Thompson ME, Muller M, Wrangham R (2009) The context of female
558 dispersal in Kanyawara chimpanzees. *Behavior* 146:629–656.
559 <https://doi.org/10.1163/156853909X413853>
- 560 Sugiyama Y (1999) Socioecological factors of male chimpanzee migration at Bossou,
561 Guinea. *Primates* 40:61–68. <https://doi.org/10.1007/BF02557702>
- 562 Sugiyama Y (2004) Demographic parameters and life history of chimpanzees at Bossou,
563 Guinea. *Am J Phys Anthropol* 124:154–165. <https://doi.org/10.1002/ajpa.10345>
- 564 Sugiyama Y, Fujita S (2011) The demography and reproductive parameters of Bossou
565 chimpanzees. In: Matsuzawa T, Humle T, Sugiyama Y (eds) *The chimpanzees of*
566 *Bossou and Nimba*. Springer, Tokyo, pp 23–34

- 567 Tutin CE (1979) Mating patterns and reproductive strategies in a community of wild
568 chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 6:29–38.
569 <https://doi.org/10.1007/BF00293242>
- 570 Tutin CE, McGinnis PR (1981) Chimpanzee reproduction in the wild. In: Graham C (ed)
571 Reproductive biology of the great apes: Comparative and biomedical
572 perspectives. Academic Press, Cambridge, pp 239–264.
- 573 Walker KK, Walker CS, Goodall J, Pusey AE (2018) Maturation is prolonged and
574 variable in female chimpanzees. J of Hum Evol 114:131–140.
575 <https://doi.org/10.1016/j.jhevol.2017.10.010>
- 576 Wallis J (1997) A survey of reproductive parameters in the free-ranging chimpanzees of
577 Gombe National Park. J Reprod Fertil 109:297–307.
578 <https://doi.org/10.1530/jrf.0.1090297>
- 579 Wittig R, Boesch C (2019) Demography and life history of five chimpanzee communities
580 in Taï National Park. In: Boesch C, Wittig R (eds) The Chimpanzees of the Taï
581 Forest: 40 Years of Research. Cambridge University Press, Cambridge, pp 125–
582 140.

- 583 Wroblewski EE (2008) An unusual incident of adoption in a wild chimpanzee (*Pan*
- 584 *troglydytes*) population at Gombe National Park. Am J Primatol 70:995–998.
- 585 <https://doi.org/10.1002/ajp.20582>
- 586

587 **Figure Legends**

588

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

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

591 Christina (XT) (right)

592

593 **Figure 1**

594

595

596 **Figure 2**

597

598

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

599

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

600 ¹ Shows the number of females who first gave birth in their natal group (i.e., the remaining females)
601 out of the total number of remaining females and nulliparous females who were estimated to emigrate.

602 ² One remaining female was estimated to emigrate to another group after the death of her first offspring.

603 ³ “6 settled as adults in the community, 5 transferred to other communities, and 3 disappeared” (Pusey
604 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

605

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

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

608 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

609

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

612 ² ? indicates estimated values

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

615 ⁴ Values were calculated up to May 2014.

616

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