

Relatedness in Wild Chimpanzees: Influence of Paternity, Male Philopatry, and Demographic Factors

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ABSTRACT In chimpanzees (*Pan troglodytes*), high-ranking males are expected to have high reproductive success and females typically emigrate upon reaching maturity. Although high average relatedness among males in the same social groups has been assumed, previous reports have indicated that relatedness among males is not necessarily significantly higher than that among females. The paternity of 11 offspring and the relatedness of 50 individuals in the M group of chimpanzees at Mahale Mountains National Park, Tanzania, were investigated using DNA analyses. We determined the fathers of 10 offspring. Two different alpha males sired a total of five offspring, whereas the other males had low reproductive success. The proportion of paternal half-sibling pairs among the 10 offspring was 15.6%. The average relatedness among mature males was significantly higher than that among mature females. The ex-

istence of an old male and the long tenure of one alpha male may have contributed to this significant difference. The average dyadic relatedness among mature natal individuals was significantly higher than that in natal-immigrant pairs in which the individuals came from different groups. The average relatedness among immigrant females was similar to that in pairs of natal and immigrant females, suggesting that the immigrants came from various groups. Thus, female transfer acts to maintain low average relatedness within the group. A comparison of our results to those from other study sites suggests that although the average relatedness among adult males does not reach the level of half-siblings, under some circumstances it can exceed the relatedness of females. *Am J Phys Anthropol* 137:256–262, 2008.

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Sex-biased dispersal and male reproductive success influence the patterns of relatedness among individuals that live in the same social group (Morin et al., 1994; Altmann et al., 1996; de Ruiter and Geffen, 1998). In most species of vertebrates, one sex typically disperses while the other remains philopatric (Greenwood, 1980). In mammals, males are typically the dispersing sex (Pusey and Packer, 1987). In primate groups in which females are commonly philopatric, e.g., macaques, the average relatedness among females is higher than that among males (Altmann et al., 1996; de Ruiter and Geffen, 1998).

In contrast, in chimpanzees (*Pan troglodytes*), it is the females that typically emigrate upon maturity (Nishida and Kawanaka, 1972; Pusey, 1979; Boesch and Boesch-Achermann, 2000). Thus, the relatedness of male chimpanzees has been assumed to be higher than that of females (Morin et al., 1994). However, in some recent genetic studies, the average relatedness among males was not significantly higher than that among females (Vigilant et al., 2001; Lukas et al., 2005). Simulations highlighted the contrast in expectations for relatedness patterns in female and male philopatric species (Lukas et al., 2005). In female philopatric species, the persistence of female lineages in the group, along with reproduction by only some of the males, both contribute to an enhancement of average female relatedness within the group. In contrast, in male philopatric species such as chimpanzees, newly immigrated females reproduce each generation and so high average relatedness among phil-

opatric males is only expected in very small groups and when reproduction is strongly skewed in favor of one or a few males (Lukas et al., 2005). However, it is important to investigate relatedness patterns in multiple wild chimpanzee groups because empirical results may differ among social groups with differing demographic histories.

High reproductive success of high-ranking males (Constable et al., 2001; Boesch et al., 2006) may result in the occurrence of half-sibling pairs within age classes in male chimpanzees. However, in an unusually large group of ~150 individuals at Ngogo, males of the same age cohort are on average only as closely related to each

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other as are males of different age cohorts, and age proximity may not be a reliable cue for paternal sibship (Langergraber et al., 2007). This may be an outcome of the large group size. In a study of western chimpanzee groups at Taï, it was shown that the reproductive success of the alpha male decreases as the numbers of competitors and synchronously receptive females increase (Boesch et al., 2006) and similar pattern has been reported in savanna baboons (Alberts et al., 2003) and long-tailed macaques (de Ruiter and van Hooff, 1993). Therefore, the percentage of kin within the same age cohort is probably lower in a large group. Langergraber et al. (2007) suggested that paternal kin effects on cooperative behaviors (Alberts, 1999; Widdig et al., 2001) may arise as a byproduct of individuals maximizing their own fitness by cooperating with age mates, who are only occasionally paternal siblings. It is thus important to investigate the effect of age proximity on male relatedness in groups smaller than that at Ngogo.

Stochastic factors such as variation in individual life histories may also influence relatedness among males and females. Females at Mahale and Taï usually emigrate from their natal groups (Nishida et al., 1990; Boesch and Boesch-Achermann, 2000). At Mahale, some females have given birth in their natal groups (Nishida et al., 1990, 2003) and some immature males have transferred to other groups with their mothers (Takahata and Takahata, 1989). Thus, differences between immigrant and natal individuals should be considered. Immigrant females usually do not risk copulating with their fathers. A female who gives birth in her natal group probably faces a high risk of inbreeding because not only her father, but also her paternal half-sibling brothers may be present. Assessing the risk of inbreeding is important from a conservation perspective because it is one of the possible consequences of dispersal limitations arising out of habitat fragmentation.

We examined the paternity and relatedness of M group chimpanzees, comprising ~60 individuals at Mahale Mountains National Park, Tanzania. Extensive demographic data have been compiled for this group (Nishida et al., 2003), making it suitable for research on relatedness. We investigated male reproductive skew, relatedness among males and that among females, the effect of age class and alpha male status on relatedness among males, and the effect of immigration on relatedness within groups. Specifically, we predict that alpha males produce a disproportionate share of the offspring, and that this may result in higher relatedness among offspring born during the tenure of the same alpha male than those born in different alpha tenures. We predict that female-biased dispersal will result in reduced average relatedness of females relative to males, but that this pattern may be affected by the presence of natal females and a lone immigrant male in this group.

MATERIALS AND METHODS

Study group and samples

We studied chimpanzees (*Pan troglodytes schweinfurthii*) belonging to the M group in Mahale Mountains National Park, Tanzania. This group has been studied since 1965 (see Nishida, 1990 for details of the study site). The birth years of all natal individuals are known.

Samples for genetic analysis were collected during 1999–2005. In particular, E.I. intensively collected samples from August to October 2003. During this sampling

period, the group comprised 51–63 known individuals, of whom the genotypes of 54 individuals were determined. Samples were collected noninvasively and consisted of feces (48 samples), urine (8), blood lost from injury (3), food wadge (2), hairs dropped by self-scratching (1), muscular tissue from a dead individual (1), and saliva from twigs that had been sucked on by chimpanzees (1). Most samples were preserved in 70% ethanol. The exceptions were 42 fecal samples that were kept in 50-ml tubes containing 20 g of silica and one hair sample that was kept in a plastic bag.

Genotyping

DNA was extracted using the phenol chloroform procedure (Hayakawa and Takenaka, 1999) or a QIAamp DNA Stool Kit (Qiagen, California, USA), QIAamp DNA Mini Kit (Qiagen), QIAamp DNA Micro Kit (Qiagen), or ISOHAIR (Nippon Gene, Tokyo, Japan) according to the manufacturers' instructions.

PCR amplifications were performed as described by Vigilant et al. (2001) and Inoue et al. (2007) using eight microsatellite loci: *D9s910*, *D11s2002*, *D2s1329*, *D12s666*, *D2s1326*, *D5s1470*, *D7s2204*, and *D7s817* (Bradley et al., 2000). The amplification products were separated using capillary electrophoresis, using an ABI Prism 3100 DNA Sequencer (Applied Biosystems, California, USA). Alleles were sized using GeneScan version 3.7 and Genotyper version 3.7 Software (Applied Biosystems).

Because the DNA extracted from noninvasive samples is typically degraded and low in concentration (Taberlet et al., 1996; Morin et al., 2001; Inoue et al., 2007), we followed the recommendations of Morin et al. (2001) to ensure accurate genotyping. Loci were typed as homozygous after the single allele was observed at total of seven times, and each allele at a homozygous locus was observed at least twice. Sample identification and genotype accuracy were confirmed by molecular sexing using the X-Y homologous gene amelogenin (Bradley et al., 2001), by verifying that all mother-offspring pairs ($N = 28$) shared an allele at each locus as expected, and by using two or three independently collected samples per individual. Of 54 individuals, three had no known sampled relatives and were genotyped using single samples.

Paternity analysis

The paternity of 11 offspring born during 1999–2005 was investigated. Paternal candidates were males who were alive and of reproductive age (at least 9 years old) at the time of conception. All of the paternal candidates of eight offspring were genotyped. For three other offspring, one paternal candidate, who was an adolescent male (<15 years of age) at the time of conception, was not sampled. Paternity was assigned by exclusion. Paternal allele(s) were deduced by comparing the mother and offspring genotypes. If the male did not possess the paternal allele(s), he was excluded as the father of that given offspring. A male was considered the likely father when the other males in the group were excluded and the male was compatible with the paternal genotypes at all of the examined loci. The confidence level of paternity and total exclusionary power of paternity assignment when the mother was known were calculated using CERVUS (Marshall et al., 1998).

TABLE 1. The results of paternity analyses

Offspring	Mother	Father	Alpha male at the time of conception	Dominance rank of father	No. of mismatches with the next best males	Confidence by CERVUS (%)
LZ ^a	LD	DG	FN	High	1	95
FV ^a	FT ^b	HB	FN	Low	3	99
PF ^a	PI ^b	AL	FN	High	4	99
XP	XT	FN	FN	Alpha	3	99
TD	TZ ^c	FN	FN	Alpha	2	95
ZH	ZL	CT	FN	Middle	2	95
IH	IK	DG or OR	FN	—	—	—
FM	FT ^b	FN	FN	Alpha	2	99
OP03	OP ^b	FN	FN	Alpha	1	99
RH	RB ^c	CD	FN	Low	1	99
CY05	CY	AL	AL	Alpha	4	99

^a One of the paternal candidates was not sampled.

^b Had mature sons.

^c Natal female.

Relatedness analyses

Using the program Relatedness 5.0.8 (<http://www.gsoftnet.us/GSoft.html>; Queller and Goodnight, 1989), dyadic relatedness (R) was estimated for all pairwise combinations of the 50 individuals (including 12 mature males and 19 mature females) who were alive in August 2003 and sampled. The program estimates relatedness by allele-sharing of pairs at all examined loci, and considers frequencies of the alleles in the population because the same alleles might not be derived from the same recent ancestor. The chance that a shared allele descends from a single common ancestral allele is stochastically different among loci. Therefore, at least 30–40 microsatellite loci are needed to obtain moderate confidence around a single pairwise estimate. In the absence of enough loci for accurate estimate of single pairwise relatedness, we may still estimate the average relatedness within categories of individuals with reasonable accuracy (Blouin, 2003; Csilléry et al., 2006).

In the analyses, mature males were sexually mature males aged 9 years or older. Mature females were those who immigrated or who were born in the M group and gave birth. We focused on mature individuals only; thus, males/females indicate mature males/females. A permutation test, which compares the normalized difference between means from 10,000 random pairs of replicates from the pooled data set, was conducted to compare relatedness between different categories of individuals.

Demographic data and male age classes

One male, MA, immigrated with his mother in childhood (Takahata and Takahata, 1989). Four natal females (AB, AK, RB, and TZ) gave birth in this group. Three old females (CA, IK, and WX) were not determined to be natal females or immigrants because they were mature when they were identified. Another 12 females immigrated from other groups. We classified dyads among males as belonging to the same (<5 years age difference) or different (≥ 5 years age difference) age classes. One male, NT, who had died had a long tenure as the alpha male, and the mothers of 8 of 12 mature males conceived while he was alpha. Dominance rank was determined by the direction of submissive pant-grunts between pairs (Bygott, 1979) and antagonistic behaviors. Males were classified as alpha, high-ranking (the next two males),

middle-ranking (the next three males), and low-ranking (the other mature males).

RESULTS

Paternity

Genotypes at eight microsatellite loci were generated for 54 individuals (Appendix 1). Paternity was assigned to 10 of 11 offspring analyzed (Table 1). For the single unassigned offspring, two paternal candidates were not excluded. All assigned fathers had no mismatches. The confidence of paternity assignment was >95% (Table 1). The average total exclusionary power in determining secondary parent was 0.997. When FN was the alpha male, he fathered 4 of 10 offspring. When AL was the alpha male, he sired one of one offspring. Overall, alpha males fathered 45.5% of offspring. Each of the five remaining offspring was fathered by a different non-alpha male, and not only high-ranking males but also middle- and low-ranking males sired infants. Among the 10 offspring whose fathers were identified, seven of 45 pairs (15.6%) were paternal half-siblings. The mothers of three offspring whose fathers were genetically identified had mature sons. Among them, inbreeding between mother and son was avoided.

Relatedness between and within the sexes

The average relatedness among males ($N = 12$ individuals, $R = 0.038$) was significantly higher than among females ($N = 19$ individuals, $R = -0.056$, permutation test; $P < 0.01$). The average relatedness among males estimated without MA, the immigrant male, increased ($N = 11$ individuals, $R = 0.091$) and was also significantly higher than among females ($P < 0.001$). To investigate whether certain individuals had more relatives in the group than is typical, the average relatedness of each individual to all other individuals of the same sex was calculated (see Fig. 1). Although the average relatedness of males to other males was often higher than that of females to other females, the average relatedness of three of the males to other males was quite low (below zero). The average relatedness of MA to other males was significantly lower ($N = 11$ dyads, $R = -0.23$) than that among all males except for MA ($N = 55$ dyads, $R = 0.091$, $P < 0.01$). The average relatedness of DE, the oldest male, to other males was the highest ($R = 0.19$). The

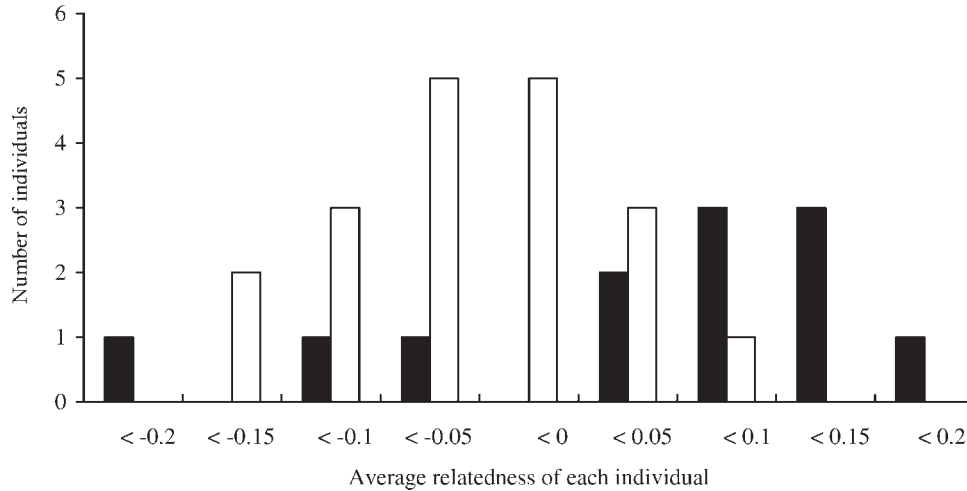


Fig. 1. Average relatedness of each individual to all other individuals of the same sex. ■/□ indicates the number of males/females who exhibited the indicated degree of average relatedness to all other males/females.

average relatedness among males except for DE ($N = 11$ individuals, $R = 0.008$) was not significantly higher than the relatedness among females ($N = 19$ individuals, $P = 0.056$). The average relatedness among males except for DE and MA ($N = 10$ individuals, $R = 0.059$) was significantly higher than that among females ($P < 0.01$).

Effect of demography on relatedness

The average relatedness of male dyads of the same age class ($N = 25$ dyads, $R = 0.053$) was not significantly higher than that across different age classes ($N = 41$ dyads, $R = 0.029$, $P = 0.58$). The average relatedness between males who were sired during the tenure of the same alpha male ($N = 28$ dyads, $R = 0.031$) was not higher than that the relatedness between males who were fathered when different males were alpha ($N = 27$ dyads, $R = 0.043$, $P = 0.17$), and was significantly higher than the relatedness among females ($P < 0.05$).

The average relatedness among natal individuals ($N = 15$ individuals, $R = 0.071$) was significantly higher than that among immigrant individuals ($N = 13$ individuals, $R = -0.028$, $P < 0.05$) and natal-immigrant pairs ($N = 195$ dyads, $R = -0.032$, $P < 0.01$). Relatedness among immigrant individuals did not differ from that among natal-immigrant pairs ($P = 0.91$). The relatedness among natal female-male pairs ($N = 48$ dyads, $R = 0.056$) was significantly higher than that among immigrant female-male pairs ($N = 144$ dyads, $R = -0.015$, $P < 0.05$).

DISCUSSION

Distribution of male reproductive success

The alpha male FN sired 4 of 10 offspring, and alpha males in total sired 45.5% of all offspring. This proportion is similar to that found at two other sites where alpha males sired 50% (Boesch et al., 2006) and 35% (Constable et al., 2001) of offspring. In contrast, each non-alpha male sired only one offspring during the study period. Low reproductive success of non-alpha males was also found in previous paternity studies at Gombe (Constable et al., 2001), where the alpha male sired 4 of 14 offspring and other males did not sire more than two

infants each. These results indicate that alpha males typically attain higher reproductive success than do non-alpha males. These results are broadly consistent with the priority of access model, which predicts that alpha males enjoy preferential access to estrous females (Altmann, 1962). Similar patterns of reproductive success of higher-ranking male have been reported in savanna baboons (Alberts et al., 2003) and long-tailed macaques (de Ruiter and van Hooff, 1993). As a consequence of these patterns, the majority of paternal half-siblings among males are limited to sons of the highest ranking males.

Difference in relatedness among sexes

In contrast to results reported from other chimpanzee study sites, in the Mahale M group, the average relatedness among males was significantly higher than that among females. The average relatedness among males was also higher than that among females at Tai, Gombe, and Budongo, but not significantly so (Vigilant et al., 2001; Lukas et al., 2005). The result at Mahale is probably due to the presence of DE, the oldest male. He had a high average relatedness ($R = 0.19$) to other males and the relatedness among males except for DE was not significantly higher than that among females. The mothers of five mature males conceived while he was the high-ranking male. He was not genetically excluded as the father of two of these five males. It is extremely difficult to ascertain relationships among adult males (Langergraber et al., 2007). One reason is the impossibility of paternity analyses given the typical lack of samples from deceased mothers and candidate sires. A second problem is the unreliability of relationship classification using dyadic relatedness estimates due to stochastic variation in the degree of allele sharing between relatives (Blouin, 2003). Thus, we can only surmise that DE, who was older than the other males by at least 14 years, might have paternal relatives such as sons or nephews.

The effect of the long tenure of one alpha male, NT, probably also affects the significant difference in relatedness among sexes. The mothers of eight of 12 mature males conceived while he was the alpha male and the average relatedness among those eight males was

TABLE 2. The percentages of paternal half-siblings within offspring cohorts

Study group	No. of individuals in group	Estimation method	No. of dyads analyzed	Paternal half-sibs (%)
M group at Mahale	60	Paternity analysis	45	15.6
Kasekela group at Gombe	45	Paternity analysis	91 (21)	11.0 (9.5)
North group at Tai	38	Paternity analysis	210 (55)	18.6 (16.3)
Ngogo group	150	Relatedness analysis	276	5.1

The percentages of paternal half-siblings at Mahale, Gombe, and Tai were calculated by the paternity of offspring (Gombe, Constable et al., 2001; Tai, Vigilant et al., 2001). The percentage of dyads in the same age cohort among adult and adolescent males at Ngogo was described by Langergraber et al. (2007). The percentages at Gombe and Tai among male offspring only are provided in parentheses. At Mahale, the data among male offspring are not shown because only 1 of 10 offspring was male.

significantly higher than that among females. There may be more paternal half-siblings among the males at Mahale than among males in the other social groups. At Tai, poaching and disease epidemics have dramatically affected the demography, which has resulted in frequent changes in the identity of the alpha male (Boesch and Boesch-Achermann, 2000). This suggests that there may not be many old males related to young males and relatively low number of paternal half-sibling pairs among mature males at Tai. The group stability at Mahale may contribute to the significant difference between relatedness among males and that among females. Thus, stochastic events such as losses or exceptionally long-term survival of particular males can strongly influence the relatedness patterns observed in chimpanzee groups.

While in chimpanzees, the relatedness among males is sometimes but not always significantly higher than that among females (Vigilant et al., 2001; Lukas et al., 2005; these results), the relatedness among females was, as expected, higher than that among males in two female philopatric societies (Altman et al., 1996; de Ruiter and Geffen, 1998). One cause of the difference between expectations and observations in the male- and female-philopatric systems may be the female-biased adult sex ratio in chimpanzees (Nishida et al., 1990; Boesch and Boesch-Achermann, 2000). The low number of old males probably leads to non-significant differences in relatedness among sexes in some chimpanzee societies. In female philopatric societies, male mortality is also greater than female mortality (Dittus, 2004). The percentage of mother-infant dyads among mature females in female philopatric societies is probably higher than that of father-infant dyads among mature males in male philopatric societies.

Effects of age proximity and alpha male tenure on relatedness

In the M group, relatedness of dyads of the same age class was not significantly higher than that of dyads across age classes, and the relatedness among males who were sired during the tenure of the same alpha male was not higher than the relatedness among males who were sired when the different males were alpha. This shows that the effect of the high reproductive success of high-ranking males on the kin structure is limited, as Langergraber et al. (2007) showed in the large Ngogo community. Although data from Ngogo showed that chimpanzee males who belong to the same age and rank class are more likely to affiliate and cooperate than those who belong to different age and rank classes (Mitani

et al., 2002), age proximity may not be a reliable social cue for paternal relatedness (Langergraber et al., 2007).

The percentages of paternal half-sibling dyads among offspring at Mahale, Gombe, and Tai were calculated using paternity assignments (Constable et al., 2001; Vigilant et al., 2001), whereas pairwise relatedness among adult and adolescent males at Ngogo was estimated because paternity data were not available for that site (Langergraber et al., 2007; Table 2). The percentages of paternal half-sibling dyads among male offspring were not different from those among offspring of both sexes combined, suggesting that sex did not affect the percentages. The percentage of paternal half-sibling dyads at Ngogo was lower than those at Mahale, Gombe, and Tai. The unusually large group size at Ngogo probably affected the low percentage of paternal half-siblings. This is consistent with the idea that high average relatedness among the philopatric sex is only expected in a very small group (Lukas et al., 2005). Overall, the percentage of paternal half-siblings of these four groups of wild chimpanzees was at most 20%. Consequently, the average relatedness among males is quite lower than the previous assumption that males are related at the half-sibling level (Morin et al., 1994).

Inbreeding risk and female dispersal

The relatedness among natal female-male pairs was significantly higher than that among immigrant female-male pairs, indicating that the risk of inbreeding was higher among natal females than among immigrant females. The relatedness among natal individuals was significantly higher than that among natal-immigrant pairs. The relatedness among immigrant females was the same as that among natal-immigrant pairs that came from different groups, suggesting that many dyads among immigrant females came from different groups. This was probably because several groups have continuously existed at Mahale (Nishida et al., 1990). At the sites where a few contiguous groups exist, the relatedness among immigrant females might be higher than that at Mahale because individuals in these groups might have a higher probability of originating from the same group, resulting in high relatedness among group members. This suggests that habitat fragmentation likely decreases genetic diversity in chimpanzees.

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APPENDIX 1. List of the individuals used in the study, including names and genotypes at eight microsatellite loci

Name	Sex	D9s910	D11s2002	D2s1329	D12s66	D2s1326	D5s1470	D7s2204	D7s817
AB	F	110/116	148/152	178/182	150/182	182/218	/	253/253	148/148
AK	F	104/104	148/148	178/182	150/182	182/206	194/194	245/253	148/152
CA	F	104/110	148/156	182/198	158/182	182/186	/	249/253	112/124
CY	F	104/116	148/152	186/198	138/154	182/214	/	253/265	144/152
EF	F	110/113	148/152	186/186	138/138	186/210	190/190	249/257	116/152
FT	F	110/113	152/156	182/182	142/154	182/182	190/194	249/253	144/148
IK	F	113/113	148/148	182/182	142/158	182/218	182/182	249/253	120/144
LD	F	116/116	148/148	186/198	138/154	206/214	182/190	249/265	144/148
MJ	F	104/113	148/148	186/198	182/182	182/182	186/190	249/249	148/152
NK	F	104/110	148/148	182/186	150/154	182/182	182/194	245/245	116/148
OP	F	104/104	144/148	186/202	154/154	186/218	186/190	233/261	148/148
PI	F	104/104	148/156	/	150/158	206/214	186/190	233/249	148/148
QA	F	104/120	148/152	178/186	154/154	/	194/194	253/261	140/144
RB	F	104/113	144/144	182/186	154/154	186/206	190/194	249/261	144/148
SY	F	110/113	148/148	182/186	138/142	182/182	190/190	241/257	116/152
TZ	F	104/110	148/148	178/198	154/154	202/206	186/190	245/249	144/148
WX	F	110/113	144/148	186/186	150/182	202/206	182/194	245/253	120/124
XT	F	104/116	148/148	182/186	138/154	182/214	186/190	249/261	144/156
ZL	F	104/113	148/148	182/198	154/158	182/202	182/194	233/253	144/152
AC	F	104/110	148/148	178/198	150/154	182/206	190/194	245/253	148/152
AQ	F	104/110	148/148	178/198	182/182	178/182	/	233/253	148/148
AT	F	104/110	144/148	178/186	154/182	186/202	186/194	245/249	116/124
CR	F	104/110	148/148	186/198	154/182	186/206	182/190	249/253	124/140
CY05	F	113/116	148/148	186/198	138/182	182/206	194/194	245/253	124/152
FM	F	110/113	148/152	182/198	142/182	182/202	190/194	249/253	140/148
FV	F	104/113	156/156	178/182	138/154	182/202	194/194	249/253	148/148
IM	F	104/113	148/156	182/198	142/158	214/218	182/182	249/253	112/120
JD	F	104/116	152/152	198/202	154/154	182/202	194/194	233/233	148/148
LZ	F	110/116	148/148	186/198	154/154	182/206	182/194	249/249	124/148
OP03	F	104/110	148/152	186/198	154/154	186/202	190/194	253/261	140/148
PF	F	104/104	144/148	186/198	158/182	206/206	190/194	233/245	124/148
RH	F	104/104	144/156	182/198	154/158	206/206	190/190	249/249	148/148
RC	F	104/113	144/148	178/186	154/154	186/202	190/190	245/261	144/148
XP	F	104/116	148/148	182/198	138/182	202/214	186/194	233/249	144/148
ZH	F	104/104	148/148	198/198	154/154	186/202	182/182	233/253	144/148
CE	M	/	148/152	198/198	154/154	/	182/194	253/265	112/152
IH	M	110/113	148/148	182/182	142/154	182/182	182/194	253/253	120/120
MC	M	110/113	148/152	186/198	154/182	182/182	190/194	249/253	140/152
OS	M	104/104	144/148	198/202	154/154	186/210	/	233/253	120/148
TD	M	104/110	148/148	198/198	154/182	202/206	190/194	233/249	148/148
AL	M	104/113	144/148	186/186	182/182	182/206	194/194	245/253	124/148
BB	M	104/104	148/152	182/182	154/154	182/202	186/190	245/257	148/148
CD	M	104/110	148/156	182/198	154/158	182/206	190/190	249/249	112/148
CT	M	104/110	148/156	198/198	154/158	186/214	182/182	245/253	112/148
DW	M	104/110	148/148	198/202	154/158	206/206	190/190	249/253	144/148
DG	M	104/110	148/148	182/198	150/154	182/210	/	249/253	120/124
FN	M	104/110	148/152	198/198	154/182	182/202	194/194	233/253	140/148
HB	M	104/104	156/156	178/182	138/154	182/202	190/194	253/253	148/152
DE	M	104/110	148/152	186/198	154/154	182/206	190/194	249/253	140/148
MA	M	110/116	144/148	178/186	138/158	182/210	194/198	245/253	116/152
OR	M	104/110	148/148	182/186	154/154	182/218	190/194	253/261	120/148
PM	M	110/113	148/156	182/198	154/154	178/182	190/194	249/249	144/148
PR	M	104/110	148/148	178/198	150/150	206/206	190/190	233/253	148/148
XM	M	104/110	148/152	186/198	138/154	178/182	190/194	249/253	140/156

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