RESEARCH ARTICLE

Living in Nonbreeding Groups: An Alternative Strategy for Maturing Gorillas

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The one-male reproductive strategy implies that maturing males are temporarily excluded from reproduction. In gorillas, these excluded males live either solitarily or in nonbreeding groups (NBGs) that are devoid of adult females. The dynamics of NBGs are not well known. In this study, which was conducted on a gorilla population (Gorilla gorilla gorilla) of 377 individuals that visited the Lokoué clearing in the Republic of Congo, we detail how the NBGs formed, and analyze their dynamics according to age-sex classes, the relatedness of members, and the origin and destination of transferring individuals. We discuss the potential benefits gained by individuals living in these groups. The NBGs included mainly immature males, most of which appeared to have migrated voluntarily from their natal groups. Some individuals (including juvenile females) came from disbanded breeding groups (BGs). Migrants preferentially joined NBGs that included a silverback male. Their dispersal patterns were not determined by their degree of relatedness, but they tended to associate with related silverbacks. In this way, the migrants could enhance their protection against predators and gain experience with different environmental conditions. By tolerating and protecting offspring, aging silverbacks could enhance their inclusive fitness. Finally, young and healthy silverbacks could increase their likelihood of forming a future BG when unrelated females joined them. Am. J. Primatol. 68:275–291, 2006. © 2006 Wiley-Liss, Inc.

Key words: nonbreeding groups; dynamics; western lowland gorilla; relatedness

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INTRODUCTION

The existence of nonbreeding groups (NBGs) has been documented in many primates (e.g., Hanuman langurs [Rajpurohit et al., 1995], geladas [Mori, 1979], and macaques [Pusey & Packer, 1987]) and other mammals (e.g., horses [Feh, 2001], elephants [Sitati et al., 2003], and wild dogs [Frame et al., 1979]). In some species, NBGs are regular features of the social organization (e.g., Nepal macaques [see Pusey & Packer, 1987] and feral horses [Kaseda & Khalil, 1996]). They have been observed in both mountain gorillas (Gorilla beringei beringei) [Fossey, 1983; Harcourt, 1978; Robbins, 2001; Stewart & Harcourt, 1987] and western lowland gorillas (Gorilla gorilla gorilla) [Gatti et al., 2004; Robbins et al., 2004], although it is believed that only one such group has occurred in eastern lowland gorillas (G. b. graueri) [Fossey, 1983; Harcourt, 1978; Robbins, 2001; Yamagiwa, 1987]. Some of these groups have been followed for years [Elliot, 1976; Harcourt & Stewart, 1987; Gatti et al., 2004; Robbins, 1996; Yamagiwa, 1987]. Their compositions are characterized by a male-biased sex ratio, the absence of reproductively active females, and a large proportion of immatures [Gatti et al., 2004; Robbins, 1995; Yamagiwa, 1987]. They have been called variously all-male groups (even if some immature females were present [Robbins, 1995]), nonreproductive groups, or bachelor groups [e.g., Harcourt, 1988; Robbins et al., 2004; Yamagiwa, 1987]. Following Gatti et al. [2004], we retain the term of “nonbreeding groups” (NBGs), as opposed to “breeding groups” (BGs), to describe groups that are devoid of adult females.

The formation patterns and dynamics of NBGs are not well known, and why some individuals join such groups remains unclear. Yamagiwa [1987] suggested that NBGs in mountain gorillas could be induced by disturbance of their habitat and poaching. However, NBGs persist when protection from poaching is developed [Sholley, 1991; reviewed in Stewart et al., 2001], and western lowland gorilla NBGs occur in areas that are free of anthropogenic disturbances [Gatti et al., 2004; Robbins et al., 2004]. Harcourt [1988] considered NBGs to be a structure induced by the one-male reproductive strategy, which excludes males from reproduction. Indeed, one-male groups represent 47–54% of BGs in mountain gorillas [Kalpers et al., 2003; McNeilage et al., 2001] and 92% of BGs in eastern lowland gorillas [Yamagiwa et al., 1993, 2003], and are the rule in several western lowland gorilla populations [Gatti et al., 2004; Robbins et al., 2004]. Data for two populations of this species [Gatti et al., 2004; Magliocca et al., 1999] show that on average, 40% of the silverbacks were unmated males that lived either as solitary (32%) or in NBGs (8%).

Some NBGs result from BGs disbanding after the death of their silverback and/or emigration of their adult females. In these cases, young individuals may stay together and constitute new social units [Robbins, 1995; Yamagiwa, 1987] in which some members are relatives [Harcourt, 1988]. Gatti et al. [2004] suggested that NBGs that include subadult females could be BGs in the making. Indeed, Watts [1992] showed that male gorillas, like some other primates [Smuts et al., 1987], can use social affiliation as a mating tactic. Similarly to Papio hamadryas males that adopt juvenile females [Kummer, 1968; Pusey & Packer, 1987], young gorilla silverbacks may develop strong bonds with subadult females with which they may later form a BG. The gorillas that emigrate from BGs and choose to integrate into an NGB instead of living solitarily could also benefit from the advantages of group living, such as better predator detection [Pusey & Packer, 1987], enhanced foraging efficiency [Rajpurohit et al., 1995; Wrangham, 1980], and improved social setting [Robbins, 2001].
In this study we detail the history of NBGs in a western gorilla population and analyze their dynamics, stressing the origin and destination of transferring individuals. We also investigate the genetic relatedness among NBG members. On this basis, we discuss the function of NBGs and the potential benefits gained by individuals that live in such groups.

MATERIALS AND METHODS

Study Site and Period

The Lokoué clearing (00°54N; 15°10E) is a 4-ha swamp area in the tropical rain forest of the Odzala-Kokoua National Park, Republic of Congo. Like other forest clearings, it is visited regularly by gorillas (see details in Gatti et al. [2004]). They were observed from a platform at the clearing edge on 515 days, for a total of 4,838 hr, from April 2001 to September 2002 and from November 2003 to March 2004.

Study Population and Data Collection

At least 377 gorillas visited the Lokoué clearing. This population included three unit types: one-male BGs, NBGs, and solitary silverback or blackback males [Gatti et al., 2004]. Age and sex classes were determined by physical, developmental, and behavioral traits, following Harcourt et al. [1980], Fossey [1982], and Watts [1990], as follows: infants (<3 yr old), juveniles (3–6 yr old), subadults (>6–8 yr old), adult females (>8 yr old), blackback males (>8–12 yr old), and silverback adult males (>12 yr old). The term “immature” refers to females under 8 years old and males less than 12 years old, and thus includes blackbacks. The gorillas were identified by physical criteria detailed in Gatti et al. [2004] from a database of more than 2,000 photos. We used the body condition and sometimes, extent of silver hairs on the flanks, neck, head, and legs to assess the age of adult males.

Because of numerous individual transfers, the composition of the NBGs changed frequently. Each group was named (L02, L03, etc.) at first observation, and the name was maintained as long as two identified members remained together. When individuals from an identified NBG associated with a solitary male, the group was given a new name (LS06, LS11, etc.). Migratory events include immigrations from other units (BGs, solitaries, or unknown units) to NBGs, emigrations from NBGs to other units, and transfers between NBGs. Gorillas that did not visit the clearing subsequently were considered emigrants, although they may have died. Even when several individuals migrated simultaneously, we recorded one migratory event for each animal, considering that each individual has the choice to follow or not follow its social partner(s). Finally, when immature gorillas joined a solitary male, only these immatures were considered immigrants, because no adult males were observed seeking the presence of younger individuals [Robbins et al., 2004] (this study).

Genetic Analyses

Fresh fecal samples (n = 24) were collected at nest sites and on the trails of identified gorillas for genetic analyses. They were desiccated and stored in sterile tubes containing silica-gel beads [Wasser et al., 1997]. Age classes were estimated on the basis of dung diameter [Schaller, 1963; Tutin et al., 1992] or by direct observation of animals defecating. DNA was extracted following the CTAB
protocol [Launhardt et al., 1998] as modified by Lathuillière et al. [2001b]. DNA from extracts was amplified by PCR at 5–8 tetranucleotide microsatellite loci using fluorescently labeled human primers (50 cycles; D1S550, D7S817, D16S2624, D18S536, vWF; annealing temperature $t^\circ = 60^\circ C$; D4S243, D10S1432: $t^\circ = 55^\circ C$; and D2S1329: $t^\circ = 50^\circ C$). Primers D1S550, D7S817, D10S1432, D16S2624, and vWF amplified DNA from gorilla feces successfully [Bradley et al., 2000]. D4S243 and D18S536 were previously used for macaques [Smith et al., 2000; Lathuillière et al., 2001a], and D2S1329 was used for chimpanzees [Bradley et al., 2000]. They were used here for the first time for gorillas (Gatti et al., in preparation). Sex was confirmed by amplification of the amelogenin locus [Bradley et al., 2001]. Individual genotypes were determined using capillary electrophoresis (ABI Prism 310, size standard ROX 500) with multiple independent PCR products made out of several extracts from the same sample [Bradley et al., 2000]. Dyadic relatedness was calculated using Relatedness software [Queller & Goodnight, 1989] and relationship categories were investigated with Kinship software [Goodnight & Queller, 1999] for all possible pairs of sampled individuals. For this, we used allele frequencies calculated from a reference population of 57–92 genotyped gorillas, depending on the locus (Gatti et al., in preparation). Mean relatedness was calculated for dyads of immatures and for silverback-immature dyads. We assessed the reliability of relatedness values using at least five loci (results not shown) with a rarefaction analysis [Altmann et al., 1996; De Ruiter & Geffen, 1998; Girman et al., 1997]. We compared these mean relatedness data for dyads of individuals in the same group (mean intragroup relatedness) and for dyads of individuals across groups (mean intergroup relatedness). Following Bradley et al. [2004], individuals were considered related when their pairwise relatedness, R, was greater than 0.2, and when the likelihood ratio for the relationship hypothesis was significant ($P<0.05$). The presence of allelic mismatches allowed a parent–offspring relationship to be excluded in related dyads.

RESULTS

NBG Histories

The histories of the 14 NBGs are described below (see details in Appendix 1A for L02, L48, and L66; 1B for L03, L07, and L26; 1C for LS11 and L17; and 1D for L61, LS06, L56, LS10, L59, and L65).

L02, a BG observed from April to July 2001, became an NBG when it lost its adult female and five immatures between July and November. L02, which permanently included an old silverback and a subadult with atrophied lips and nose, visited the clearing 19 times until March 2004. During this time, it received several migrants, but none remained in it for long.

L48 (four visits to the clearing in November 2001) was composed of a silverback and a subadult female. The subadult female later joined NBG L02 and the silverback visited the clearing alone until the end of the study.

L66 (two visits), which was first observed in August 2002, was composed of a solitary blackback that had resided temporarily in L02, a previously solitary old silverback, and a juvenile (the latter two came from the same disbanded BG). The juvenile was previously seen alone once in the clearing, whining like a distressed infant (as described by Schaller [1963]). In September 2002, the blackback and the juvenile were seen without the silverback that was alone in November 2003.
L03 (26 visits) included seven immatures in April 2001. It gradually lost all of its members, except for two blackbacks (February 2002). These blackbacks stayed together, separated, met again (August 2002), and eventually lived as solitaries after at least November 2003.

L07 originated from a BG observed in April 2001. From June to September, this BG successively received two clusters of three, and then five, young migrants from L03 and L26, respectively. It lost its adult female with her infant between 21 December 2001 and 6 January 2002. After that, NBG L07 was seen 25 times at the clearing until August 2002. In December 2003, one of its blackbacks was seen alone, and in March 2003 one of its subadult males was observed in LS11. Its silverback looked very old (loss of hair on top of his head and shoulders, weak muscle structure, wrinkled skin) and probably died.

L26 included five subadult males that visited the clearing on two occasions around mid-June 2001. They all mixed with L07 a few days later.

L17 (four visits) included six immature gorillas in June 2001. Later, in November 2001, they were all seen in LS11.

LS11 included, in November 2001, 14 individuals (one solitary silverback, the six immatures from L17, one subadult from L02, and six immatures of unknown origins). Its composition changed during its 20 visits to the clearing. Two blackbacks became solitary (December 2003 and March 2004). In March 2004 this group included 15 individuals with the same silverback and three blackbacks.

L61 (six visits) included eight immatures in March 2002. It lost two subadults that formed LS06, and a blackback that temporarily integrated into a BG before it began to live solitarily (November 2003). Other group members were not identified again.

LS06 (11 visits), first observed in June 2002, included four gorillas resulting from the association of a solitary silverback (known since May 2001), two subadult males from L61, and a juvenile from the same disbanded BG as the members of L66. This juvenile had serious facial skin lesions. In November 2003, LS06 included two new subadult males. In 2004, two subadult males that were present when the group formed were seen alone once. One of them was seen in L02 in March 2004, whereas the other was not seen again.

L56 (three visits) included four immature males in January 2002. In August, three of them had associated with the solitary silverback S10 and had formed an NBG called LS10 (see below).

LS10 was seen once in August 2002. It included two subadult males and one juvenile male from L56 (see above), and a solitary silverback identified since May 2001. After September 2002 this silverback lived alone and the immatures were not observed again.

L59 (five visits) consisted of one silverback and one subadult female in March 2002. The following August, it received one juvenile and in September, it became a BG as three adult females joined it. Two of them came from a known BG.

L65 (3 visits) included one silverback with three subadult females in July 2002. It was not seen after August 2002.

Structure of the NBGs

Sixty-six individuals belonged to NBGs. They included 86.5% of immatures, 44% of subadults, 23% of juveniles, 20% of blackbacks, and 13% of silverbacks (Table I). Eighty-one percent of the sexed individuals (n = 54) were males, and six of the 11 groups for which all individuals were sexed included only males at a given time (L02, L03, L26, L56, LS10, and LS06; Appendix 1). Seventy-eight
<table>
<thead>
<tr>
<th>Age/sex classes</th>
<th>Silverback male</th>
<th>Adult female&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Blackback male</th>
<th>Sub-adult total</th>
<th>Sub-adult male</th>
<th>Sub-adult female</th>
<th>Juvenile total</th>
<th>Juvenile male</th>
<th>Juvenile female</th>
</tr>
</thead>
<tbody>
<tr>
<td>NBGs, % (n = 66)</td>
<td>13.6 (n = 9)</td>
<td>– (n = 13)</td>
<td>19.7 (n = 29)</td>
<td>44 (n = 18)</td>
<td>62 (n = 5)</td>
<td>17.2 (n = 15)</td>
<td>22.7 (n = 4)</td>
<td>44.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>55.5&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>BGs, % (n = 228)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>16.2 (n = 37)</td>
<td>51.3 (n = 117)</td>
<td>3.1 (n = 37)</td>
<td>16.2 (n = 6)</td>
<td>16.2 (n = 19)</td>
<td>51.3 (n = 30)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total % of migrations (n = 61)</td>
<td>1.6 (n = 33)</td>
<td>4.9 (n = 21)</td>
<td>24.6 (n = 7)</td>
<td>47.6 (n = 21)</td>
<td>36.1 (n = 30)</td>
<td>3.3 (n = 19)</td>
<td>21.3 (n = 4)</td>
<td>3.3 (n = 15)</td>
<td>11.5</td>
</tr>
<tr>
<td>No. of emigrations from NBG (n = 33)</td>
<td>1</td>
<td>0</td>
<td>9</td>
<td>18</td>
<td>14</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>No. of immigrations into NBGs (n = 21)</td>
<td>0</td>
<td>3</td>
<td>3</td>
<td>8</td>
<td>6</td>
<td>0</td>
<td>7</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>No. of transfers between NBGs (n = 7)</td>
<td>–</td>
<td>–</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

<sup>a</sup>Adult females immigrating to non-breeding groups from breeding groups.

<sup>b</sup>Only weaned individuals are figured, see Gatti et al. [2004].

NBG, non-breeding groups; BG, breeding group.
percent of the sexed subadults \( n = 79 \) were males, whereas the sex ratio of juveniles (60% of which were sexed) was balanced \( (\chi^2 = 7.348, df = 1, P = 0.007; \chi^2 = 1.111, df = 1, P = 0.739, \text{respectively}; \text{Table I}) \).

The Lokoué population observed from April 2001 to September 2002 [Gatti et al., 2004] included 37 silverbacks and seven blackbacks living in BGs, seven silverbacks and seven blackbacks living in NBGs, and 20 silverbacks and 11 blackbacks living solitarily. The number of males older than 8 years did not differ significantly from the number of adult females. For the same period, the population of NBGs included significantly more males (sex ratio F/M: 0.14 and 2.72, respectively; \( \chi^2 = 51.553, df = 1, P < 0.001 \)), less silverbacks and more blackbacks \( (\chi^2 = 14.297, df = 3, P = 0.003) \), and a greater proportion of subadult males than females \( (\chi^2 = 9.868, df = 1, P = 0.002; \text{Table I}) \).

As a result of frequent migrations, 33 different compositions of NBGs were observed; 24 included a single silverback and only three included subadult females. The remaining nine groups included only immatures (Appendix 1). Overall, 27 included at least one subadult (var. 0–10), 20 included at least one blackback (0–4), and 19 included at least one juvenile (0–5).

**Dynamics of the NBGs**

We recorded 61 migratory events (33 emigrations, 21 immigrations, and seven transfers (Table I)). The number of migration events per individual varied from 0 to 3, and approximately half of the individuals of the NBGs (31/66) migrated at least once. Taking into account the representation of each age-sex class, we observed that all age classes migrated in similar proportions \( (\chi^2 = 0.624, df = 3, P = 0.101) \) and females migrated as often as males \( (\chi^2 = 0.004, df = 1, P = 0.948) \).

We identified the group left by the migrant and the destination of the migrant in 46 migratory events (Fig. 1). Thirty-nine percent of the emigrations

![Fig. 1. Origin and destination of migrants to and from NBGs. ?: Unknown origin or destination.](#)
from an NBG (n = 28) concerned immatures (seven males and four unsexed individuals) that joined a solitary silverback, and this led to the formation of new NBGs. Thirty-two percent concerned immatures (six subadult males, one unsexed subadult, and two juvenile females) that joined two different BGs. These immigrations were followed by the departure of the single adult female of these BGs and thus induced the formation of two new NBGs. Finally, 29% of the emigrations concerned males (five blackbacks, two subadults, and one silverback) that became solitaries. One of the subadult solitaries visited the clearing alone for at least 1 month (nine visits), whereas the other was seen only once before it was observed 4 days later in the L02 NBG (Appendix 1). Ten of the 11 immigrations (four juveniles, three adult females, two subadult males, and one blackback) concerned gorillas leaving a BG, and the 11th involved a solitary blackback. All these immigrants, except one juvenile female and the solitary blackback, joined NBGs including a silverback. Four immature migrants came from three disbanded groups, and three came from stable BGs. None of these emigrations were due to the death of the leading silverbacks that were seen thereafter either as solitaries, in an NBG, or leading their residual group. Finally, the seven transfers among NBGs concerned five males (three blackbacks and two subadults) and two immature females (one subadult and one juvenile). Overall, 76% of the subadults and juveniles emigrated from an NBG that was devoid of silverbacks (n = 25 emigrations; Appendix 1) and 97.5% joined a group including a silverback or joined a solitary silverback (n = 37 immigrations). Similarly, the three adult females immigrated into NBGs with a silverback. The two juvenile females that emigrated from an NBG joined a BG.

The migratory events concerned one individual in 61% of the cases. Simultaneous migrations were observed on seven occasions. They included 24 gorillas from seven different groups and involved 13 subadults (10 males and three unsexed individuals), five juveniles, three adult females, and three blackback males.

Among the five NBGs that included only immature gorillas, some members of three groups (L17, L56, and L61) joined a solitary silverback and formed new NBGs (LS11, LS06, and LS10). One group (L26) merged entirely with a BG, which subsequently lost its adult female (L07), and one group (L03) disbanded. The three NBGs that included a silverback (L02, L66, and L07) originated from three BGs led by old silverbacks that lost their adult females. Two disbanded after they received an influx of immatures (eight of the nine migrants sexed were males). Only one immature stayed with the silverback in L02, and the L66 silverback later became solitary.

Overall, three NBGs disbanded: L03 (see above), which included only immatures, disbanded after the emigration of its youngest members and two blackbacks that became solitaries; L48 (a silverback and a subadult female) disbanded after the female joined another NBG with a silverback; and L59 (a silverback, a subadult female, and an immigrant juvenile) became a BG following the immigration of three adult females, two of which came from the same disbanded BG and were related (S. Gatti, unpublished data). The origin and the fate of L65 NBG remained unknown.

As a result of these changes, known individuals stayed in NBGs for periods ranging from a few days to over a year. Two groups (L66 and L26) were not observed with the same composition for more than 10 days. Two blackbacks (L03) remained together for at least 10 months, and eight immatures remained with the same silverback for 28 months (LS11). Finally, the association of a silverback and a subadult lasted at least 35 months (L02; Appendix 1A). On the whole, groups
that were composed of only immatures were the most unstable, and those that included a silverback were the most stable. Lastly, NBGs were more unstable than BGs. Indeed, from April 2001 to September 2002, both types of groups showed 43 migratory events, whereas NBGs included only 62 gorillas and BGs included 267 weaned gorillas ($\chi^2 = 35.014$, df = 1, $P<0.001$).

**Relatedness Among Members of NBGs**

We estimated the relatedness among the 24 gorillas sampled from five NBGs (i.e., 36% of the population and 40–75% of group members; Table II). Globally, 90% of the 59 sampled intragroup dyads of immatures involved unrelated gorillas. Related immatures were found in two NBGs: three dyads involving three immatures in L07, and three dyads involving five immatures in LS11. Two related immatures in L07 were immigrants from an NBG that was devoid of silverbacks (L03 or L26 in June 2001; Appendix 1B). They migrated together from the same unit or independently.

Three of the four silverbacks tested were related to some immatures in their group (Table II). The L02 silverback was related to, and not excluded as the father of, one subadult male, but he was not related to the subadult female that transferred from NBG L48. This silverback and his putative son constituted the most stable association in the group, within which other members did not stay long. Similarly, the L07 silverback was related to, and not excluded as the father of, one of the immigrating immature males and one juvenile female. This female was already a member of the BG led by this silverback, which became an NBG following the emigration of its adult female. The LS11 silverback was related only to the immigrant juvenile female; however, the father/daughter relationship was excluded.

Overall, the mean intragroup relatedness among immatures ($R = 0.031$; 59 dyads) did not differ significantly from the mean intergroup relatedness among

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**TABLE II. Relationships Within Genotyped Groups**

<table>
<thead>
<tr>
<th>Group identity</th>
<th>L02</th>
<th>L03</th>
<th>L07</th>
<th>LS11</th>
<th>LS06</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group size at collection date</td>
<td>5</td>
<td>4</td>
<td>12–9</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Presence of silverback</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>No. of genotyped individuals per group (n = 25)*</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>No. of related immature pairs per group/total no. of possible immature pairs</td>
<td>0/1</td>
<td>0/3</td>
<td>3/10</td>
<td>3/45</td>
<td>–</td>
</tr>
<tr>
<td>No. of related SB-immature pairs/total no. of possible SB-immature pairs</td>
<td>1/2</td>
<td>–</td>
<td>2/5</td>
<td>1/10</td>
<td>0/1</td>
</tr>
<tr>
<td>No. individuals unrelated to any of the other group members</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

*The same juvenile was typed in two different groups (in L03 and LS11, see Appendix 1).
immatures ($R = 0.043; 131$ dyads). On the contrary, the mean intragroup relatedness between silverbacks and immatures ($R = 0.223; 18$ dyads) was significantly greater than the mean intergroup relatedness between silverbacks and immatures ($R = 0.0184; 66$ dyads). It was also significantly higher than the mean intragroup relatedness among immatures. These results suggest that most immatures dispatched among NBGs regardless of their relatedness, and that some immatures tended to associate with related silverbacks.

DISCUSSION

Our study shows that NBGs include significantly more males compared to BGs, that blackback males are overrepresented in NBGs, and that some NBGs contain only males. Such groups occur in many primate species that live in one-male BGs (e.g., gelada baboons [Mori, 1979], patas [Chism & Rowell, 1986], blue monkeys [Cords, 1987], capped langurs [Stanford, 1991], Thomas’s langurs [Steenbeek et al., 2000], and mona monkeys [Glenn et al., 2002]), in some species with multimale structures (e.g., rhesus macaques [Boelkins & Wilson, 1972], bonnet macaques [Simonds, 1973], and Japanese macaques [Sugiyama, 1976]), and in species in which both social systems are observed, such as Hanuman langurs [Rajpurohit et al., 2004] and gorillas [Robbins, 2001]. Approximately 50% of the mountain gorilla BGs are multimale. Kalpers et al. [2003] estimated that about 12% of the groups were nonbreeding, and that solitary males represented about 4% of the individuals in the population. Similar proportions were observed in lowland gorilla, although one-male BGs predominated ($\chi^2 = 0.063, df = 2, P = 0.969$). About 13% of the units were NBGs, and 6% of the individuals were solitary [Gatti et al., 2004; Magliocca et al., 1999; Parnell, 2002]. At Lokoué, a greater proportion of individuals lived in NBGs than in the two other western lowland gorilla populations studied, and males emigrated at an early age from their natal group. Since the age-sex structures of the three populations are comparable [Gatti et al., 2004], we cannot invoke a deficit of females to explain the differences in the proportions of individuals living in NBGs. Similarly, since the stability of BGs at Lokoué is comparable to that of other populations [Robbins et al., 2004] (S. Gatti, unpublished data), group disintegration cannot explain the higher dispersal of immatures. We hypothesize that transfers of individuals between units would be favored by the high density of the Lokoué population and the subsequent high frequency of inter-unit encounters (F. Levréro, unpublished data).

NBGs: As an Alternative Social Structure for Immatures

Harcourt and Stewart [1977] and Harcourt [1978] pointed out that male emigrations from mountain gorilla BGs resulted from their gradual peripheralization and reduced relationships among group members, especially with the silverback. Yamagiwa [1987] and Robbins [1996] showed that males living in NBGs had more frequent social interactions and a lower risk of serious wounds than those living in BGs. These results were recently confirmed in a study of captive gorillas [Pullen, 2005]. Similarly, Steenbeek et al. [2000] showed that levels of aggression among Thomas’s langur males living in all-male bands were lower than in bisexual groups. Yamagiwa [1987], Robbins [1995, 1996], and Waterman [1997] also suggested that living in NBGs could enhance information exchanges and the development of social skills. However, so far nobody has tested
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whether males that live in NBGs have a greater likelihood of reproducing than solitary males.

At Lokoué, 72% of the blackback males did not live in BGs; 61% of these males were solitaries and 39% lived in NBGs. In addition, nearly 65% of the subadult males lived in NBGs [Gatti et al., 2004]. Maturing gorillas that live in NBGs instead of living alone could benefit from the experience of silverbacks, especially from their knowledge of the environment and their protection against predators [Pusey & Packer, 1987]. This is supported by the facts that subadult and juvenile gorillas avoided living alone, that those belonging to NBGs devoid of a silverback tended to join either a solitary silverback or a group including a silverback, and that groups including a silverback were more stable than groups of immatures.

Although there were more subadult males than females in the NBGs, juveniles of both sexes were equally represented. Most of these juveniles, especially females, migrated after their natal groups had disbanded and did not seem to migrate voluntarily from stable BGs, as the subadult males appeared to do. Indeed, we never observed active eviction of these males from their natal group, whereas such evictions are known in species that live in one-male groups [Pusey & Packer, 1987].

The low level of relatedness observed among immatures in the NBGs may be explained by the fact that immature migrants from a given BG did not necessarily join the same groups, and, moreover, they could transfer again between NBGs afterwards. Similarly, the two habituated all-male groups of mountain gorilla were formed by unrelated individuals [Robbins, 1996; Yamagiwa, 1987]. The fact that members of NBGs change frequently indicates that social bonds are weaker in these groups than in BGs. In Thomas’s langurs, Steenbeek et al. [2000] showed that such groups are not as stable as bisexual groups. The absence of clear dominance hierarchies, evictions, and harassments in NBGs (e.g., mountain gorillas [Robbins, 1996]) may also facilitate transfers among groups.

NBGs: A Strategy for Aging Males to Increase Their Inclusive Fitness?

Watts [1992] reported that the oldest silverback in a multimale group of mountain gorillas gave agonistic support only to his relatives, whereas the younger silverback tried to retain nonrelative immigrants as potential mates. Watts [1996, 2000] hypothesized that an aging male would gain an advantage by accepting the presence of related immatures, because their chances of survival to adulthood would increase, and his inclusive fitness would increase. Our results on the relatedness between silverbacks and immatures in NBGs tend to show a predominant role of silverbacks in the dispersal strategy of immatures. In several cases, immature offspring preferred to stay with their putative father after their natal group disbanded, or to join a related silverback. However, the occurrence of some long-lasting NBGs that included unrelated members suggests that an aging male with no reproductive opportunities may prefer to maintain a social life even with unrelated animals rather than remain alone. This could explain why two aging males that led BGs tolerated an influx of immatures that were unrelated to them, even if this influx hastened the departure of their unique females.

NBGs: A Mating Strategy for Young Silverbacks?

Three NBGs in our study population included only one silverback and one to three subadult females. These three males appeared to be in good health, and
their groups, except the one that disbanded, may have evolved later into BGs after the females reached maturity. One of these groups became a BG following the immigration of three adult females, whereas the subadult females in the other group did not reach sexual maturity during our study. Unfortunately, we were not able to sample these groups to test relatedness between the silverbacks and females. However, relatedness analyses in other NBGs showed that the two oldest genotyped immigrant females were unrelated to the silverback. Conversely, the two youngest genotyped juvenile females that were present in two NBGs were related to the silverback. These results tend to show that living in NBGs may constitute a mating strategy by healthy males to attract adult and subadult females. Immigrations of mountain gorilla females into NBGs were recorded in three cases, but their arrivals disrupted the stability of these groups [Elliot, 1976; Harcourt, 1988; Watts, 1990]. In some primate species, males in NBGs may form alliances to increase their chances of entering bisexual groups or gaining a harem residency (e.g., red howlers and Hanuman langurs [Pusey & Packer, 1987; Rajpurohit et al., 1995]). Takeovers of a one-male BG by males in NBGs have never been observed in gorillas.

CONCLUSIONS

Our results show that NBGs constitute temporary and unstable structures that are induced by many migratory events involving blackback males, subadults, and juveniles of both sexes. NBGs also include aging and young adult males. Consequently, all gorillas in the study population may belong to an NBG at some point in their lifetime (except for infancy and female adulthood). NBGs harbor some males that have been excluded from BGs by the gorilla reproduction system, and NBGs represent an alternative strategy for immature animals leaving their natal groups. The active choice of migrants to join a silverback is determined by their relatedness to him rather than to other immatures, and suggests that they require the benefit of his experience and protection against predation. Our results also suggest that aging males may benefit from tolerating immature gorillas. In addition, NBGs may increase the likelihood that young adult males will form BGs. On the whole, the occurrence of NBGs indicates that more benefits are derived from living in a group than from living alone.

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REFERENCES


APPENDIX 1

This appendix describes the dynamics of the NBGs during the study period (April 2001–March 2004). The group compositions (A–D) are given for their first visit and for every change in composition (Appendix 1).
Appendix 1. Lxx = name of group; Sxx = name of solitary male; LSxx = name of group including a former solitary male; Sol: solitary male. The date of the last visit of a group is written near the group (dd/mm/yy).

- Group disbanded;
- Transfer occurred in the clearing;
- We considered that L17 joined silverback S11 when he was still solitary, since solitary S11 and L17 had already been seen together during a previous visit to the clearing.