Received: 21 March 2018 | Revised: 22 June 2018 | Accepted: 1 July 2018
DOI: 10.1002/ajp.22898

RESEARCH ARTICLE

WILEY AMERICAN JOURNAL OF PRIMATOLOGY

Long-term group membership and dynamics in a wild western lowland gorilla population (*Gorilla gorilla gorilla*) inferred using non-invasive genetics

Laura Hagemann | Christophe Boesch | Martha M. Robbins | Mimi Arandjelovic | Tobias Deschner | Matthew Lewis* | Graden Froese† | Linda Vigilant

Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Correspondence
Laura Hagemann, Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
Email: laura_hagemann@eva.mpg.de

Funding information
Max Planck Society; Tusk Trust; Berggorilla und Regenwald Direkthilfe e. V.; United States Fish and Wildlife Service Great Ape Conservation Fund

The social organization of a group-living animal is defined by a balance between group dynamic events such as group formation, group dissolution, and dispersal events and group stability in membership and over time. Understanding these processes, which are relevant for questions ranging from disease transmission patterns to the evolution of polygyny, requires long-term monitoring of multiple social units over time. Because all great ape species are long-lived and elusive, the number of studies on these key aspects of social organization are limited, especially for western lowland gorillas (*Gorilla gorilla gorilla*). In this study, we used non-invasive genetic samples collected within an approximately 100 km^2 area of Loango National Park, Gabon to reconstruct group compositions and changes in composition over more than a decade. We identified 98 gorillas and 11 mixed sex groups sampled during 2014–2017. Using published data from 85 individuals and 12 groups surveyed between 2005 and 2009 at the same locality, we tracked groups and individuals back in time. The identification of 11 silverbacks via parentage analyses and the genetic tracking of 39 individuals across studies allowed us to infer six group formations, five group dissolutions, and 40 dispersal events within 12 years. We also observed four groups persisting across the sampling periods with a maximum inferred existence of nearly 17 years and exhibiting variation in membership stability. Our results highlight the variation in composition and stability among groups of western lowland gorillas and illustrate the power of non-invasive genetic sampling for long-term monitoring.

KEYWORDS
dispersal, group dissolution, group formation, social organization, stability, transfer

*Current address: Greater Mahale Ecosystem Research and Conservation, P.O. Box 60118, Dar es Salaam, Tanzania.

†Current address: Nicholas School of the Environment, Duke University, P.O. Box 90328, Durham, NC 27708.

1 | INTRODUCTION

The social organization is a key component of the social system of an animal taxon (Kappeler & Schaik, 2002). It is defined by the size, composition, cohesion, and genetic structure of the social units (Altizer et al., 2003; Kappeler & Schaik, 2002). Social groups are comprised of multiple adult individuals coordinating their activities and sharing space. By influencing access to mates, resources, and members of other social units, the social organization influences the fitness of individuals, and thereby shapes the evolution of populations and species.

The social systems of humans and our closest living relatives, the African great apes, exhibit marked variability today. For example, chimpanzees and bonobos form multimale multifemale communities typified by female dispersal and a promiscuous mating system largely without long-term breeding associations (summarized in Nishida & Hiraiwa-Hasegawa, 1987 but see Gruber & Clay, 2016; Langergraber, Mitani, Watts, & Vigilant, 2013). In contrast, although multimale groups are common in mountain gorillas (*Gorilla beringei beringei*), western lowland gorillas (*Gorilla gorilla gorilla*) live predominantly in one-male groups featuring dispersal by both sexes and a polygynous mating system with long-term associations between males and females (Harcourt & Stewart, 2007b).

To understand the social dynamics of a species, it is relevant to consider not only the typical structure of a species' social group, but also the group's stability. The term group stability encompasses both the temporal existence of a group, and the rate and manner of changes in group membership. For example, chimpanzee groups do not typically exchange males, and thus the Y-chromosomes present in groups may acquire mutations over generations resulting in group-specific genetic profiles (Arandjelovic et al., 2011; Langergraber et al., 2007; Moore, Langergraber, & Vigilant, 2015). Such profiles have been used to estimate that chimpanzee groups may persist as long as 2,000 years (Langergraber et al., 2014). In contrast, gorilla groups typically form when one or more females begin a long-term association with a mature silverback male, and such a group dissolves upon the death of the silverback (Harcourt & Stewart, 2007a), although approximately half of mountain gorilla groups contain more than one male and those groups typically continue after the death of the dominant male (Robbins, 1995; Robbins et al., 2013). In any system, the membership of groups changes according to births, deaths, immigration, and emigration. The frequency and distance of dispersal events define the degree of connectivity between groups, which has direct implications for disease transmission patterns (Genton et al., 2017; Nunn, Thrall, Stewart, & Harcourt, 2008) and shapes the genetic structure of a population (Fünfstück et al., 2014; Guschanski, Caillaud, Robbins, & Vigilant, 2008; Leslie et al., 2015; Roy, Gray, Stoinski, Robbins, & Vigilant, 2014). Humans and apes typically display a pattern of isolation by distance in which individuals in geographically proximal groups are on average more related than individuals in geographically more distinct groups (Fünfstück et al., 2014; Roy, Gray, et al., 2014; Slatkin, 1993).

In contrast to the well-studied mountain gorillas of the eastern species, the western lowland gorillas exhibit only the presumably ancestral structure of mixed sex groups containing a single adult silverback male (Gatti, Levréro, Ménard, & Gautierhion, 2004; Parnell, 2002; Yamagiwa, Kahekwa, & Basabose, 2003). In both gorilla species, maturing males and females may disperse (summerized in Robbins et al., 2004). In western lowland gorillas, male gorillas become solitary or join all-male groups before eventually acquiring females and forming a mixed sex group (Levréro et al., 2006) while female gorillas transfer directly from one group to another or join a solitary male and form a new group (Stokes, Parnell, & Olejniczak, 2003). Although unusual among mammals, female secondary transfer is common in western lowland gorillas (Stokes et al., 2003). Groups may disband quickly following to the death of the silverback and the subsequent dispersal of the females or slowly by the successive departure of females, who may transfer between groups multiple times in their lives (Harcourt & Stewart, 2007a; Stokes et al., 2003).

Western lowland gorillas are long-lived, elusive animals living in dense habitat, which makes the direct observation of multiple groups over a long period of time especially challenging. Habituation allows for detailed behavioral observation but it is time- and labor-intensive (Williamson & Feistner, 2003) and so only one or a limited number of groups is typically habituated at a field site simultaneously. Although valuable information on aspects of the social system of western lowland gorilla can be gained by direct observation of multiple groups in swampy forest clearings, called bais (Breuer et al., 2010; Gatti et al., 2004; Parnell, 2002; Robbins et al., 2016; Stokes et al., 2003), they spend a limited fraction of their time (around 1%) at the bai and the history or fate of individuals appearing or disappearing from the groups that visit the bai may be difficult to ascertain.

One approach used to infer the dynamics of multiple western gorillas groups employs genetic analysis of non-invasively collected sources of DNA. Such non-invasive samples can be collected with minimal disturbance and are routinely used in wildlife studies (reviewed in Schwartz, Luikart, & Waples, 2007; Waits & Paetkau, 2005) for applications ranging from genetic mark-recapture analyses to abundance estimation (Arandjelovic et al., 2015; Guschanski et al., 2009; Lampa, Henle, Klenke, Hoehn, & Gruber, 2013; Miller, Ward, & Schultz, 2015; Roy, Vigilant et al., 2014; Stansbury et al., 2014), tracking of individuals (Jeffery, Abernethy, Tutin, Anthony, & Bruford, 2007) or tracking evolutionary histories of populations (Fünfstück et al., 2014; Roy, Arandjelovic, et al., 2014). Notably, the use of non-invasive genetic analysis to monitor the dynamics of multiple western gorillas over a limited time (Bradley, Doran-Sheehy, & Vigilant, 2007) or several years has been demonstrated (Arandjelovic et al., 2010; Arandjelovic, Head, Boesch, Robbins, & Vigilant, 2014). Paternity analyses suggested that all individuals in one western lowland gorilla group were sired by the silverback of the group (Bradley, Doran-Sheehy, Lukas, & Boesch, 2004). Over a 5-year period, Arandjelovic, and colleagues inferred the minimal group composition, changes in group composition and group dynamic events of 12 groups in a 132 km^2 research area at Loango National Park, Gabon. This study gave initial insights into the frequency of group formations,

dissolutions, and dispersal events and suggested a highly dynamic system. However, because rare events such as dispersal are inherently stochastic, further study is needed to assess stability, and group persistence and achieve a more comprehensive view of the group dynamics.

In this study we use non-invasive genetic samples to track individual gorillas and ascertain social groups of wild western lowland gorillas over a 12-year period to better understand patterns of group formation, disintegration, dispersal patterns, and stability of groups. We combine published data from samples collected in 2005–2007 and 2009 (Arandjelovic et al., 2010, 2014) with new data generated from samples collected in 2014–2017 within an approximately 100 km^2 area of Loango National Park. Tracking of individuals and the reconstruction of groups and pedigrees enables us to reveal dynamic processes that occurred over a decade. Our specific aim is to investigate group composition, group stability, and dispersal events between groups. We address temporal stability by examining the number of groups that persist over the entire study period, the number of groups that dissolved, the number of groups that formed, as well as the number of individual movements these changes imply. This allows us to make inferences on the connectivity of the groups as well as on the duration of male-female bonds, providing valuable comparative information for understanding the evolution of hominid social organization.

2 | METHODS

2.1 | Study site and sample collection

Gorilla fecal samples were collected between January 2014 and February 2017 within an approximately 100 km^2 area bordered by a large lagoon to the Northeast and the Atlantic Ocean to the Southwest (Figure 1). Collection of samples occurred upon discovery of gorilla trails or nest samples, as detailed in the supplementary material.

We divided the sampling area into 25 grid cells of two by 2 km each. To ensure equal coverage of the sampling area we first

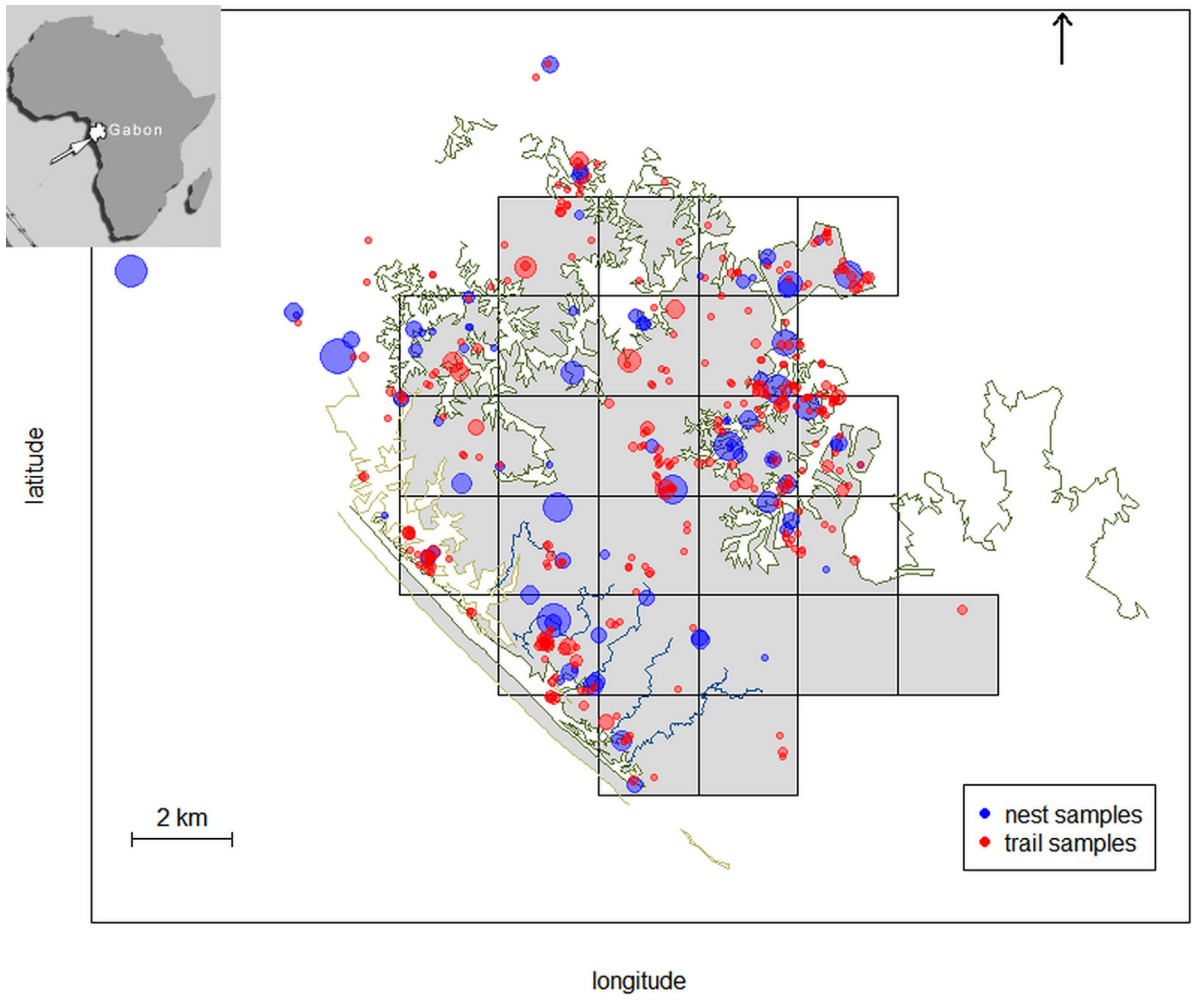

FIGURE 1 The ~932 samples used in this study, collected during 2014–2017. The squares represent the grid cell and the border of the study area; lines represent the border of the lagoon and affiliated swamps, the border of the savanna or rivers. Gray is the forest habitat within the study area. The samples are designated as nest or trail samples and the area of circles is proportional to the number of samples found at the respective location

implemented a systematic sampling design in which each grid cell was visited once in the course of an approximately three month sampling period, termed "sweep." Each cell was searched using a 12 km reconnaissance walk (recce) with adjustments for inaccessible areas. We also attempted tracking if fresh signs of apes were found, thus disregarding the grid cell boundaries. This systematic approach yielded very few samples (on average 33 per sweep of the 100 km^2 area). We thus modified the protocol by prioritizing our effort in an adaptive manner. We hierarchically selected areas to be searched based on i) presence of fresh gorilla signs; ii) presence of high levels of preferred food; and iii) length of time since the last search. For this study no animal was captured or tested and no regulations of the Deutsches Tierschutzgesetz or the US Public Health Service Policy on Humane Care and Use of Laboratory Animal were violated. The study was conducted in accordance with ASP principles for the ethical treatment of non-human primates and German law.

2.2 | DNA extraction, quantification, and amplification

We extracted 932 samples using the EURx® Gene Matrix Stool DNA kit version 1.2 (ROBOKLON, Berlin, Germany). The standard protocol was modified for dried feces by using between 30 and 100 mg instead of 200 mg of sample as template and an initial overnight incubation. We did two extraction negatives with each batch of 22 samples.

We first amplified 188 extracts in three independent PCR reactions at 13 microsatellite loci and a sex-determining locus. Results showed that many extracts failed to amplify or amplified inconsistently. We thus quantified the amount of amplifiable mammalian DNA in the extracts using a quantitative PCR (Morin, Chambers, Boesch, & Vigilant, 2001) as recently detailed (Granjon, Rowney, Vigilant, & Langergraber, 2017).

Extracts with high amounts of DNA (>100 pg/μl) were amplified in three independent PCR reactions at 13 microsatellite loci and for sexing at the X–Y homologous segment of the amelogenin gene (Bradley, Chambers, & Vigilant, 2001) using a two-step PCR method (Arandjelovic et al., 2009) but with the modification that the second-step PCRs were performed in four multiplex combinations with three to four loci each instead of singleplex PCR reactions (Arandjelovic et al., 2015) (see Supplementary material, Table S1). Extracts with low amounts of amplifiable DNA (5–100 pg/μl) were first subjected to a "test oplex" of four replicate amplifications each at three microsatellite loci and amelogenin in a one-step multiplex PCR. Only extracts that amplified in at least two replicates for heterozygotes and three replicates for homozygotes at a minimum of two out of the four loci were further analyzed in quadruplicate at the remaining nine loci in a two-step mplex as described above. All PCR reactions were conducted in 96-well plates along with three to seven PCR negatives and one PCR positive. A trial showed that extracts estimated to have a very low amount of DNA (< 5 pg/μl) were unlikely to pass the test oplex screening step and we therefore did not attempt to genotype them further.

We electrophoresed the amplicons at a dilution of 1:200 on an ABI PRISM 3130 Genetic Analyser using ROX labeled GENESCAN 400HD (Applied Biosystems, Foster City, CA) as an internal standard and used the software GeneMapper version 3.7 (Applied Biosystems) to visualize and score the results manually. A heterozygote locus was confirmed if both alleles were observed in at least two independent replicates, homozygotes were confirmed if seen in at least three independent replicates (McCarthy et al., 2015) and no other allele was observed. Since allelic dropout is the most important source of genotyping errors (Miller, Joyce, & Waits, 2002; Morin et al., 2001; Navidi, Arnheim, & Waterman, 1992; Pompanon, Bonin, Bellemain, & Taberlet, 2005) we calculated the average dropout rates for all loci. The number of replicates needed to confirm homozygosity with 99% certainty (Arandjelovic et al., 2009; Morin et al., 2001) was three or four for extracts with estimated amounts of amplifiable mammalian DNA of <25 pg/ng while three were always sufficient for extracts with higher estimated amounts.

2.3 | Identity analyses and comparability with previously published genotypes

To ensure consistent allele calling between studies we re-genotyped three extracts previously typed in Arandjelovic et al. (2010). We compared genotypes to find repeatedly sampled individuals using the "identity analysis" function of the program Cervus (version 3.0.7) (Kalinowski, Taper, & Marshall, 2007). We first compared genotypes generated from samples collected during the current study and only considered genotypes as unique if they showed at least two mismatches to any other genotype. For every exact match the pID (probability of identity) and the pIDsib (probability of identity among siblings) were calculated (Waits, Taberlet, & Luikart, 2001). The frequency of highly related dyads in populations of large vertebrates is expected to be low (Csilléry et al., 2006) and so we considered genotypes with zero mismatches and a pIDsib value <0.01 to be from the same individual and combined them to create consensus genotypes. We next compared the resulting consensus genotypes with the genotypes of individuals identified during the previous studies while allowing for one mismatch in order to account for genotyping inconsistency between the two studies.

2.4 | Verifying field assignment of gorilla samples

Gorillas and chimpanzees are sympatric at the research site and so we used the genotypes to verify the species identity of our putative gorillas samples using STRUCTURE version 2.3.4 (Arandjelovic et al., 2010; Evanno, Regnaut, & Goudet, 2005; Pritchard, Stephens, & Donnelly, 2000). Previously verified gorilla and chimpanzee genotypes were used as references (Arandjelovic et al., 2010, 2014).

2.5 | Group assignment

We assigned group composition as follows. First, samples of similar decay state found on the same day within 20 m proximity to each other were considered to originate from individuals from the same group. For this we used a function in R defining clusters of samples in 20 m

proximity to at least one other sample collected on the same day (kindly provided by R. Mundry) (R Development Core Team, 2017). Next, we used patterns of co-association in order to improve our knowledge of group composition. If, for example, samples from individual A, B, and C were found in association and later samples from individual A, B, and D were found together we assumed all four individuals to be from the same group (Arandjelovic et al., 2010, 2011). The method was validated reconstructing the research group Atananga which was habituated since 2013. We defined the first detection of a group as the date when either multiple samples from different individuals were found together or when a sample of a female that was later attributed to the group was found alone because females are not expected to be solitary. Individuals that were never found in association with a male gorilla were considered to have unknown group association. One male was found unassociated on two independent occasions on a trail and was therefore considered a solitary silverback.

2.6 | Pedigree reconstruction

Using Cervus (version 3.0.7) (Kalinowski et al., 2007) we reconstructed parent–offspring trios found within all genotypes completed at eight or more loci that were identified in this and the previous study. Due to the lack of information on age all individuals were potential offspring, all males potential fathers and all females potential mothers (Arandjelovic et al., 2014). For the simulation we used the same parameters (simulation for 10,000 offspring with 150 candidate mothers, 150 candidate fathers estimating 30% of both being sampled; 1% genotyping error rate) as in Arandjelovic et al. (2014) but with a new allele frequency file (91% genotype completeness). We implemented 90% and 95% as the critical values for the log likelihood statistic. Further details of the parent–offspring trio analysis are described in the supplementary material. Based on the trio analyses we designated the group silverback as the male member that sired at least one offspring.

2.7 | Changes in group number and composition over time

We assessed changes in group presence and composition over a 12-year time span by detecting dynamic processes within this study as well as across this and the previous study (Arandjelovic et al., 2010, 2014). We assumed that a group formed during the unsampled period when it was only found during the present study but not the previous. Conversely, we inferred group dissolution when a group was detected during the previous study but not during the present and we sampled former members in different groups. We defined groups as still existing when the group's silverback and at least one other member of the group were found together during both studies. In case the silverback could not be identified during the first study, we assumed group persistence if one male and one female were still present in the group and the male was inferred to be the silverback during the second study. In order to minimize the risk that the fate of a group is inferred incorrectly either because groups were simply not found during one of the studies or because we misinterpret the outcome we concentrate on mixed sex groups that were found multiple times within the study area. We inferred movements of individuals between social units under the assumption that group composition was constant within the sampling periods respectively if no explicit evidence suggested otherwise. Female transfers can be voluntary or involuntary following the death of the silverback and the dissolution of the group (Stokes et al., 2003). We cannot reliably differ between the two options since we do not know the sequence of events. Nevertheless, we describe evidence such as multifemale transfers or infant survival to provide informed suppositions. We differentiate between male dispersal to become solitary and male movement between social units, but refer to both combined as dispersal events. We infer that a male has dispersed if a male is initially found in a mixed sex group and subsequently is found repeatedly alone, in another mixed sex group or in an all-male group without being found in the first mixed sex group again. Despite our careful approach we point out that our study necessarily represents a minimum depiction of group number, composition, and dispersal at Loango. Possible false positive inferences of transfers resulting from misattribution of group membership in the context of a group encounter cannot be completely ruled out.

2.8 | Rates of group formation, disintegration, female transfer, and group persistence

We estimated the rates of group formation, disintegration and female transfer per group year for the entire time period (2005–2017) and for both study periods individually (2005–2009 and 2014–2017). We focused on mixed sex groups sampled multiple times within the study area and only included transfers if the female was sampled within the group of emigration and the group of immigration. We divided the number of formations, dissolutions, and female transfers, respectively, by the number of group years, which is the sum of years individual groups were sampled (last date of detection-first date of detection) within the period of interest. For the previous study, samples were collected between 2005 and 2007 and for two groups in 2009, while samples were collected between 2014 and 2017 for this study. Therefore, dissolutions and formations in the unsampled period, between 2007 and 2014, cannot be dated accurately which introduces uncertainty in the calculation of group years for the overall period. To overcome this issue we estimated minimum group years by using the first and last sampling dates as strict bounds. We also estimated maximum group years by assuming all relevant groups formed the last date of sampling in 2007 and disintegrated the first day of the second sampling period. For example, if a group was only sampled between February 2014 and December 2016, the minimum number of group years is the time between these dates so 2.8 group years. However, assuming that the group formed in October 2007 (the first unsampled month), we obtain a value of 9.2 group years as the maximum number of group years. In addition, we differentiate between observed group years and minimum inferred group existence (Supplementary material,

Figure S2). For the minimum inferred group existence we also use the detection of offspring sired within a group to infer that the group has already been in existence for at least 4 years, that is given the typical lack of detection of feces from individuals younger than 3 years (Guschanski et al., 2009; Roy, Vigilant et al., 2014). Furthermore, the detection of individuals related as parent–offspring between groups can also inform group histories given that female offspring typically disperse as sub-adults, between 6 and 8 years of age (Stokes et al., 2003) and adult females occasionally leave juvenile offspring between four and 6 years of age behind (Harcourt & Stewart, 2007a).

3 | RESULTS

3.1 | Discrimination of individuals and parent–offspring trios

We produced genotypes complete at five or more loci from 79% (732 of 932) of the samples. After comparison of these new genotypes with one another as well as 85 gorilla genotypes found previously (Arandjelovic et al., 2010, 2014) and a reference set of sympatric chimpanzee genotypes, we derived from 681 gorilla samples a final data set of 98 new gorilla genotypes complete at an average of 12 loci. In comparison to the previous study, 39 gorillas were found in both data sets, meaning that 46 and 59 gorilla genotypes were found only in the first and second study, respectively, corresponding to a recapture rate of at least 46% between studies and a total of 144 gorilla genotypes from the study area between 2005 and 2017.

Parentage analysis revealed 35 parent–offspring trios. For 30 trios, all members were in the same group, and all trios within the same group had the same male as father (Figure 2). We thereby identified the silverback of 11 out of 17 mixed-sex groups found between 2005 and 2017. Four males sired one offspring each, one male sired two, one male sired three, two males sired four, one male sired five, one male sired six, and one male sired seven offspring. Similarly, most (n = 17 of 25) assigned mothers had one offspring, while six had two, and two assigned mothers had three offspring.

3.2 | Gorilla group composition 2014–2017

We identified 11 mixed sex groups consisting of two to 14 individuals (Table 1, Figure 2). The inferred composition of the habituated research group (Atananga) matched the known composition with the exception of the typical lack of genotypes from infant offspring below the age of 3 years (three individuals below three and two not born at the beginning of the sampling period 2014–2017, personal

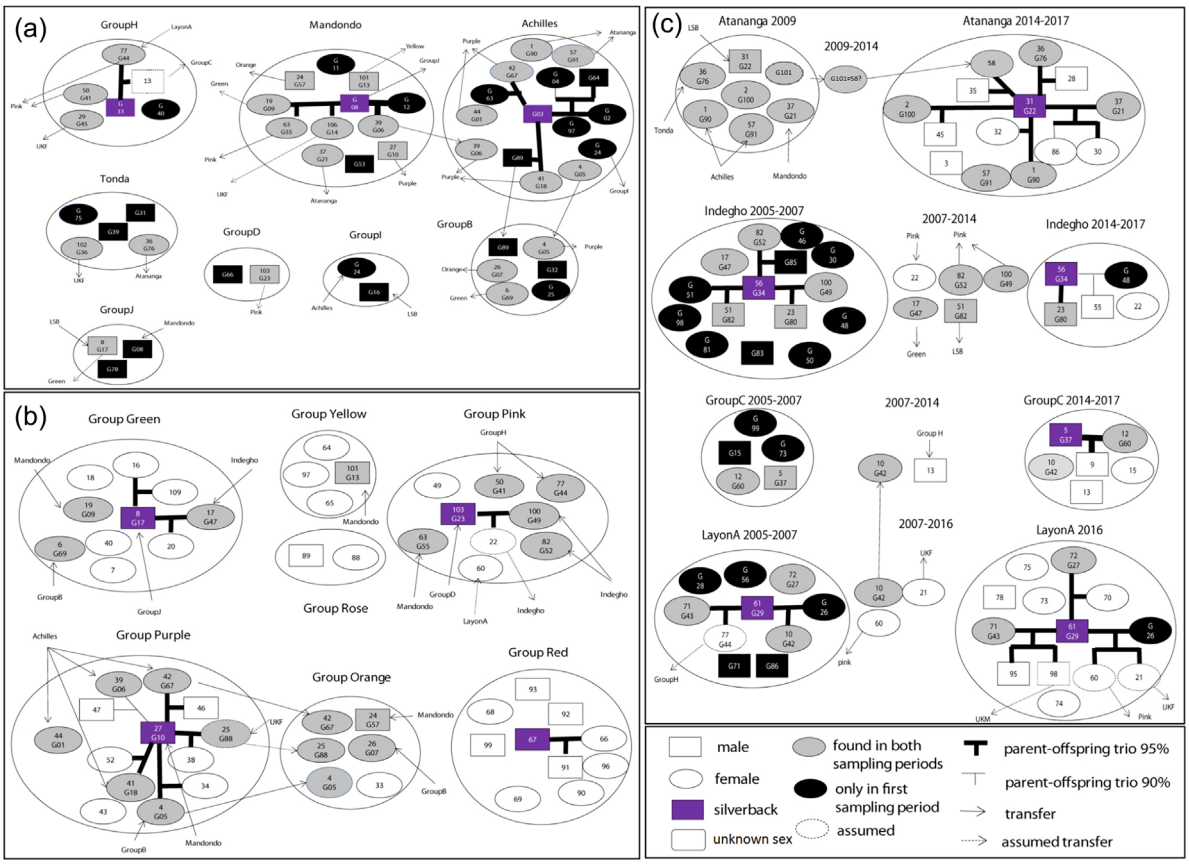

FIGURE 2 Detailed group composition and changes in group composition of all groups found in this and the previous study. (a) Groups only found during the previous study and possibly dissolved, (b) groups only found during this study and possibly formed, (c) groups found during both sampling periods. ? = In one case (G101, 58) an individual was a likely but not confirmed match. To be conservative, we here assume she is the same individual and does not represent a transfer

TABLE 1 Summary of the group composition, sampling period, and inferred fate of all groups identified in this and the previous study

Group	Minimum no. individuals (M, F)	Minimum no. offspring sired by silverback	No. of times sampled[a]	First sampling	Last sampling	Minimum group existence[b] (years)	Minimum inferred group existence[c] (years)	Inferred fate
Period 1 (2005–2009)								
Mandondo	10 (4, 6)	3	7	02/2005	03/2006	1.0	6.5	Dissolved
Achilles	14 (3,11)	4	10	02/2006	09/2007	1.6	5.3	Dissolved
GroupI	2 (1, 1)	0	1	11/2006	11/2006	0.0	0.0	Formed, left
GroupB	3 (1, 2)	0	3	02/2005	04/2009	4.2	4.2	Dissolved
GroupH	5 (1, 4)	1	2	01/2007	04/2007	0.3	0.3	Dissolved
Tonda	5 (2, 3)	0	1	09/2006	11/2006	0.2	0.2	Dissolved
GroupJ	3 (3, 0)	0	1	12/2006	12/2006	0.0	0.0	Dissolved
GroupD	2 (2, 0)	0	1	06/2006	11/2006	0.4	0.4	Dissolved
Periods 1 and 2								
Atananga -1	7 (1, 6)	0	3	03/2009	04/2009	7.8	7.8	Formed
Atananga -2	14 (5, 9)	6	5	03/2014	01/2017			Persisted
Indegho -1	15 (5, 10)	3	7	09/2006	09/2007	9.9	13.4	Persisted
Indegho -2	4 (3, 1)	4		01/2015	08/2016			
LayonA -1	9 (3, 6)	2	4	09/2006	03/2007	10.2	16.9	Persisted
LayonA -2	9 (3, 6)	7	1	05/2016	12/2016			
GroupC -1	5 (2, 3)	0	3	03/2005	11/2006	11.8	11.8	Persisted
GroupC -2	6 (3, 3)	1	10	02/2014	01/2017			
Period 2 (2014–2017)								
Group Green	10 (1, 9)	2	11	11/2014	12/2016	2.1	6.1	Formed
Group Pink	8 (1, 7)	1	4	11/2015	01/2017	1.2	9.0	Formed
Group Purple	12 (3, 9)	5	20	02/2014	11/2016	2.8	6.4	Formed
Group Orange	6 (1, 5)	0	10	02/2014	12/2016	2.8	2.8	Formed
Group Rose	2 (1, 1)	0	1	01/2016	01/2016	0.0	na	na
Group Yellow	4 (1, 3)	0	1	11/2016	11/2016	0.0	na	na
Group Red	11 (5, 5, 1 unk. sex)	1	1	02/2017	02/2017	0.0	4.0	na

[a]Number of different days at least two members of the group were found together.
[b]Minimum existence of groups based on first and last sampling.
[c]Minimum existence of groups based on sampling and indirect evidence.

observation M. Robbins). Four groups were only found once while two or more individuals of the remaining seven groups were found together on two to 20 different days within the 3 year sampling period (see Supplementary material, Figure S1). In addition to the 11 groups, nine females and five males could not be associated with any group. One of the five males was sampled alone twice and is thus considered a solitary silverback.

3.3 | Group persistence, group dissolution, and group formations

The persistence, dissolution and formation of mixed sex groups were inferred via tracking of groups and individuals within and between the two study periods (Figure 2). Four of 14 mixed sex groups for which we could infer their fate (Atananga, Indegho, GroupC, and LayonA) persisted for at least 7 years (Table 1). Sampling of offspring within the group within 1 year of first detection suggests that the estimated group ages for Indegho and LayonA should be increased by around 4 years to roughly 14. In addition, in 2007 a female offspring assigned to a parent-pair within group LayonA had already transferred from that group to GroupH. A minimum dispersal age of 6 years implies that LayonA likely formed before 2,000 for a minimum inferred group age of nearly 17 years.

The remaining 10 groups were only sampled within either study period at intervals between ~1 month and ~4 years which led us to the assumption of their dissolution or formation. In addition to previously

inferred group dissolutions ($n = 2$, Mandondo and Achilles) (Arandjelovic et al., 2010, 2014), we inferred three more recent dissolutions (GroupH, Tonda, and GroupB). The five dissolutions within 12 years and 56–103 group years approximate a disintegration rate of 0.05–0.09 disintegrations per group year. Two of the dissolutions occurred during the previous study in the 10.5 group years between 2005 and 2009, while none occurred within this study in the 16.7 group years between 2014 and 2017. This produces a rate of 0.19 disintegrations per group year during the previous and zero during the present study. The dissolutions of the Mandondo and Achilles groups were inferred to occur around 2006 and 2008, respectively, and we were able to find all three identified offspring of G08 (Mandondo's silverback) during this study in different groups, but none of the four G03 (Achilles' silverback) offspring, including one which had already dispersed to GroupB, were detected (Figure 2). The silverback of the dissolved Mandondo group was found later during the previous study in an all-male group, and he was the only one of five silverbacks that was detected again after the assumed dissolution of his group. We found one pair and one quartet of females from the Achilles group in two different groups subsequently. Similarly, two females from GroupH were found in the same new group (Group Pink) and the only assigned offspring (a male) was found in a mixed sex group (GroupC) and thus presumably transferred as a juvenile or sub-adult. In contrast to these findings of individuals ending up in the same group, two former Mandondo females, two female offspring and three males were all found in different groups. Because transfer of multiple females to the same group occurs in the context of group dissolution due to the death of the silverback and infanticide cases have been inferred for immigrant females traveling with dependent offspring (Harcourt & Stewart, 2007a; Stokes et al., 2003), these results are consistent with a sudden dissolution of the Achilles and possibly GroupH but not Mandondo group.

In addition to two previously inferred group formations (Atananga and GroupI) (Arandjelovic et al., 2010, 2014) we inferred the formation of four mixed sex groups (Orange, Green, Pink, and Purple) (Figure 2). This equates to a formation rate of 0.06–0.11 formations per group year for the total period 2005–2017, 0.19 formations per group year between 2005 and 2009 and zero between 2014 and 2017. GroupI was already assumed to have left the study area before 2007 (Arandjelovic et al., 2010) but all of the other groups were found on multiple occasions between 2014 and 2017. No offspring were detected in Group Orange but three females transferred from Group Purple to Group Orange, at least two of them in 2015. This may suggest a recent formation date for Group Orange and a minimum group age of 3 years. We found parent–offspring trios in each of Groups Green, Pink, and Purple; in Group Green all members of the parent–offspring trio were found within the group, in Group Pink the parents were found within the group but the offspring was found in Indegho and in Group Purple the father and offspring were found within the group but three different mothers were found in Group Orange (Figure 2). Consequently we infer that Groups Green and Purple existed at least 4 years before first sampling and are therefore at least 6 years old. For Group Pink we assume a formation date at least 7 years prior to the first sampling, wherefore the group existed for at least 9 years. All four groups still existed at the end of 2016 hence we cannot infer the total group lifespans. Three additional mixed sex groups (Group Red, Group Yellow, and Group Rose) were found only once or outside of the study area. We detected offspring only in Group Red, wherefore we assume the Group is at least 4 years old. For Group Rose and Group Yellow, however, we can make no inferences regarding their temporal persistence.

3.4 | Group membership

The repeated detection of individuals within and between the two sampling periods allowed us to detect individual movements between groups. In total we inferred 40 dispersal events by 34 different individuals that could be associated to a social unit prior to and post dispersal (Table 2). Of these, 33 dispersal events were between mixed sex groups while the remaining seven involved either a solitary silverback or a presumed all-male group. Five dispersal events were inferred from parent–offspring trios of disparate group membership (Figure 2), and for 35 dispersal events we sampled each individual first in association with the original social unit and subsequently in the social unit it joined. The majority (28 of 40) of dispersals were by females. Of the 23 females who dispersed, one female was inferred to have transferred three times, three females two times, and the remaining 19 transferred one time each. Six of the 23 females were sired by the silverback of the group of emigration, and a further seven were of uncertain paternity. For the remaining 15 transfers by 13 females, the emigrant females were not fathered by the silverback of their previous group, and so represent secondary dispersals. Ten females emigrated from four groups that still exist while the remaining 18 transfers originated in five groups that subsequently ceased to exist. In one case the transfer occurred prior to the dissolution of the group Achilles and for the remaining 17 the sequence of events is unknown; however, for nine females emigrating from Achilles and

TABLE 2 Overview of all detected dispersal events by males and females

	Female	Male	Total
No. dispersal events	28	12	40
No. dispersals inferred by parent–offspring trio	4	1	5
No. of individuals	23	11	34
No. presumed natal dispersals	6	3	9
No. presumed secondary dispersals	15	6	21
No. dispersals between mixed sex groups	28	5[a]	33
No. dispersals with group of emigration dissolved[b]	18	6	24

[a]In three cases we assume a solitary period in between; in another two we assume the dispersal of a subadult individual.
[b]Not including all-male groups or social units, the sequence of events is not resolved.

GroupH results described in the previous section suggest involuntary transfers after the sudden dissolution of the group.

In addition to the 28 female transfers, we detected 12 dispersal events by males that occurred in varied contexts. Three males dispersed from Mandondo group and were subsequently found in Groups Yellow, Orange, and Purple, respectively, although they may have been solitary during the interval between studies. Two of them were identified as the silverback of their new group; interestingly, neither was the offspring of the Mandondo silverback. Similarly, we also found two males dispersing from their natal groups (GroupH and Achilles) to the already existing mixed-sex groups GroupB and GroupC. It is likely that both males were subadult when they dispersed, as subadult males have been observed to enter breeding groups in other populations (Robbins et al., 2004; Stokes et al., 2003). In addition to dispersals between mixed-sex groups, we observed three males becoming solitary or a member of an assumed all-male group and four males, that had been solitary or members of an assumed all-male group, acquiring females, and thereby forming new groups. One male could not be assigned to a group in either sampling period which might indicate a prolonged solitary period.

We next examined whether dispersal events occurred at a steady rate over the study period. As previously reported, 1 dispersal event was inferred to occur prior to the beginning of the previous study (before-2005) and 12 dispersal events of seven females and five males occurred during the first study period (Arandjelovic et al., 2014). During the period between studies (2009–2014) we infer that 25 dispersal events occurred. Of these, 16 female transfers and 6 male dispersals might be linked to a group dissolution or formation while two female transfers and one male dispersal event are not. During the latest data collection period from 2014 to 2017, we inferred only two dispersal events. In sum, we estimated female transfer rates as 0.26–0.48 female transfers per group year for the whole period 2005–2017 (Supplementary material, Figure S2), 0.67 and 0.12 female transfers per group year for the periods 2005–2009 and 2014–2017, respectively. Along with the 28 female transfers we observed 12 male dispersal events within 12 years but it should be acknowledged that solitary silverbacks may have a lower detection rate, so that the observed number of dispersal events for males may be more downwardly biased than it is for females. Overall we estimate a rate of 2.3 transfers and 1.0 dispersal events per year for females and males, respectively, in this population of at least 98 gorillas ranging over approximately 100 km^2 but it is clear that this is a minimum rate and that it encompasses a high degree of temporal variation.

4 | DISCUSSION

4.1 | Group temporal stability

The genetic monitoring of 19 gorilla groups over a 12-year period revealed remarkable variation in persistence of groups and the stability of their membership. Our estimates are necessarily minimum values, but we found direct and indirect evidence suggesting one group persisted for nearly 8 years, two groups for at least 11 years, and one that may have existed as long as 17 years. Male tenures as long as 12.3 years has been reported in western lowland gorillas (Breuer et al., 2010). However, information is limited by the duration of studies, and the existence of groups for more than 20 years has been observed (M. Manguette, Mbeli Bai, personal communication). We also inferred six group formations, five group dissolutions and the breakup of two presumed all-male groups which led us to a dissolution rate of 0.05–0.09 dissolutions per group year and formation rate of 0.06–0.11 formations per group year based on 56–103 group years. At Mbeli Bai, a site where multiple groups are monitored as they appear at a clearing, two group formations and five group dissolutions were inferred over the course of 6.5 years representing 62.6 group years, yielding a rate of 0.08 group dissolutions and a 0.03 group formations per group year (Robbins et al., 2004; Stokes et al., 2003). While the observed rate of group dissolution is comparable to our finding, the rate of group formation in Mbeli appears lower than in Loango, which could, however, be influenced by the different monitoring methods. It is also notable that we find substantial variation in formation and dissolution rates between time periods. In the previous study (2005–2009) we inferred 0.19 disintegrations and 0.19 formations per group year as compared to zero formations and zero disintegrations per group year between 2014 and 2017. Although the differences in rates may reflect real fluctuations in group dynamics, stochastic variance due to the rarity of events is likely to play a role, highlighting the need for further long-term observations.

4.2 | Group membership stability

We observed variation in membership stability between gorilla groups independent of dissolution and formation. One extreme is the Atananga group, where no changes in group membership except for births were detected over a 7.8 year period of time. In contrast, five changes were inferred over 9.9 years in the Indegho group. This could potentially be due to different stages in the group lifecycles with Atananga representing a “mature” stable group and Indegho an older, “senescent” group (Parnell, 2002). Overall we inferred a female transfer rate of 0.26–0.48 female transfers per group years for the whole study period and large variation between the studies (0.67 female transfers per group years in the previous and 0.12 in this study). This difference is in accordance with our observation that the majority of female transfers (17 of 28) are connected to the dissolution of the group, and these events were more frequent in the first study period. For comparability between studies we concentrated on transfers for which the female was sampled in both origin and destination groups. Female transfer was reported with zero transfers in Maya Nord within 36 group years (Magliocca, Querouil, & Gautier-Hion, 1999) and 13 female transfers within 62.6 group years resulting in 0.21 female transfers per group year in Mbeli bai (Stokes et al., 2003). Again the rates found in Mbeli are at the lower end compared to what we observed in Loango. This may suggest that there is variance in group stability between populations but could also be due to differences in methodologies.

Comparisons are difficult due to differing life histories and social organizations but information from other species with a polygynous

mating system also reveals a high degree of variation in stability. For example, hamadryas baboon society is based upon one-male units, which persist for approximately one to 6 years (Pines, Chowdhury, Saunders, & Swedell, 2015). Across species, variation in stability of polygynous groups has been suggested to be linked to variation in resources and male competitive ability. For example, in polygynous bats the group stability may be related to the properties of the roost (Kunz & Lumsden, 2005; Muñoz-Romo, Herrera, & Kunz, 2008). In another example, the stability of the typically one-male breeding groups formed by reindeer during the mating season apparently varies with the relative social ranks of the males across groups (L'Italien et al., 2012). In a cross-cultural study examining the stability of pair bonds in humans, the level of polygyny, male contribution to subsistence, and male aggression were invoked as explanations for variation in pair bond stability (divorce rates), whereby the degree of polygyny was positively correlated with pair bond stability (Quinlan & Quinlan, 2007).

Polygynous groups with a single male are rare in primate societies (Shultz, Opie, & Atkinson, 2011) and one reason could be the higher temporal instability of one-male compared to multimale groups. Certain species exhibit some mixture of one-male and multimale social organization. One example is the Thomas's langur, which has a group life cycle similar to that of western lowland gorillas with the difference that in the langurs, some groups transform into age-graded multimale groups, and aggressive takeovers by outside males can occur. Interestingly, group takeovers or inheritance by subordinate males within the group were not observed (Steenbeek, Sterck, de Vries, & van Hooff, 2000). Therefore, the group's persistence still equals the dominant male's tenure but the presence of multiple males might extend the male tenure (Steenbeek et al., 2000) which in turn increases group temporal stability. Although multiple silverback males have rarely been observed in mixed sex western gorilla groups (Robbins et al., 2016), evidence suggests the presence of presumed subadult males unrelated to the silverback within a group (Arandjelovic et al., 2014; Levréro et al., 2006). Given the routine presence of multiple silverback males in mountain gorilla groups (Robbins, 1995; Robbins et al., 2009; Stoinski et al., 2009; Yamagiwa et al., 2003), further study is needed to determine how western gorilla groups lead by a single silverback may come to contain unrelated males.

For the future, we recommend more consistent monitoring with regular intervals and complimentary data from a limited number of habituated groups and camera traps to increase precision (Head et al., 2013). Several sampling periods with shorter intervals in between would help to increase temporal resolution and to resolve the sequence of events such as dissolutions and female transfer. Use of data on more habituated groups will eventually allow investigating the question of whether human presence has an effect on dispersal patterns. The use camera trap data might aid inference on the age structure of the population. In conclusion, genetic monitoring over 12 years provides insights into the very varied dynamics of individual movement and group stability in western gorillas, and our results contribute to an emerging picture of extreme variation in the social dynamics of this long-lived species.

ACKNOWLEDGMENTS

We thank the Agence Nationale des Parcs Nationaux (ANPN) and the Centre National de la Recherche Scientifique et Technique (CENAREST) of Gabon for permission to conduct our research in Loango National Park. Funding was provided by the United States Fish and Wildlife Service Great Ape Conservation Fund, Tusk Trust, Berggorilla und Regenwald Direkthilfe e. V., and the Max Planck Society. We also thank S. Lucchesi, F. Baguette, T. Maubec, J. Richardson, K. Judson, K. Sweeney, A. Granjon, K. Mannion, M. Basile, E. Theleste, K. Dierks, C. Herf, and all involved trackers from Waka National Park for help with sample collection and importation. We thank A. Nicklisch for sample extraction and her and K. Wuttig for laboratory support, S. Ban for French lessons and R. Mundry for help with Figure 1 and the cluster analyses. We also thank V. Städele, H. Jang, M. Manguette, E. Wright, N. Seiler, J. Lester, A. Heilman, V. Kandza, A. Granjon, N. Nurmi, and V. Maibach for helpful input and discussion.

ORCID

Laura Hagemann http://orcid.org/0000-0003-1901-0121
Mimi Arandjelovic http://orcid.org/0000-0001-8920-9684

REFERENCES

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., . . . Pulliam, J. R. C. (2003). Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 517–547. https://doi.org/10.1146/annurev.ecolsys.34.030102.151725

Arandjelovic, M., Bergl, R. A., Ikfuingei, R., Jameson, C., Parker, M., & Vigilant, L. (2015). Detection dog efficacy for collecting faecal samples from the critically endangered Cross River gorilla (*Gorilla gorilla diehli*) for genetic censusing. *Royal Society Open Science*, *2*(2), 1–14. https://doi.org/10.1098/rsos.140423

Arandjelovic, M., Guschanski, K., Schubert, G., Harris, T. R., Thalmann, O., Siedel, H., & Vigilant, L. (2009). Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. *Molecular Ecology Resources*, *9*(1), 28–36. https://doi.org/10.1111/j.1755–0998.2008.02387.x

Arandjelovic, M., Head, J., Boesch, C., Robbins, M. M., & Vigilant, L. (2014). Genetic inference of group dynamics and female kin structure in a western lowland gorilla population (*Gorilla gorilla gorilla*). *Primate Biology*, *1*, 29–38. https://doi.org/10.5194/pb-1-29-2014

Arandjelovic, M., Head, J., Kühl, H., Boesch, C., Robbins, M. M., Maisels, F., & Vigilant, L. (2010). Effective non-invasive genetic monitoring of multiple wild western gorilla groups. *Biological Conservation*, *143*(7), 1780–1791. https://doi.org/10.1016/j.biocon.2010.04.030

Arandjelovic, M., Head, J., Rabanal, L. I., Schubert, G., Mettke, E., Boesch, C., . . . Vigilant, L. (2011). Non-invasive genetic monitoring of wild central chimpanzees. *PLoS ONE*, *6*(3), 1–11. https://doi.org/10.1371/journal.pone.0014761

Bradley, B. J., Chambers, K. E., & Vigilant, L. (2001). Accurate DNA-based sex identification of apes using non-invasive samples. *Conservation Genetics*, *2*(2), 179–181. https://doi.org/10.1023/A: 1011847528045

Bradley, B. J., Doran-Sheehy, D. M., Lukas, D., & Boesch, C. (2004). Dispersed male networks in western gorillas. *Current Biology*, *14*, 510–513. https://doi.org/10.1016/j

Bradley, B. J., Doran-Sheehy, D. M., & Vigilant, L. (2007). Potential for female kin associations in wild western gorillas despite female dispersal.

Proceedings of the Royal Society B: Biological Sciences, *274*(1622), 2179–2185. https://doi.org/10.1098/rspb.2007.0407

Breuer, T., Robbins, A. M., Olejniczak, C., Parnell, R. J., Stokes, E. J., & Robbins, M. M. (2010). Variance in the male reproductive success of western gorillas: Acquiring females is just the beginning. *Behavioural Ecology Sociobiology*, *64*, 515–528. https://doi.org/10.1007/s00265-009-0867-6

Csilléry, K., Johnson, T., Beraldi, D., Clutton-Brock, T., Coltman, D., Hansson, B., . . . Pemberton, J. M. (2006). Performance of marker-based relatedness estimators in natural populations of outbred vertebrates. *Genetics*, *173*(4), 2091–2101. https://doi.org/10.1534/genetics.106.057331

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software structure: A simulation study. *Molecular Ecology*, *14*(8), 2611–2620. https://doi.org/10.1111/j.1365–294X.2005.02553.x

Fünfstück, T., Arandjelovic, M., Morgan, D. B., Sanz, C., Breuer, T., Stokes, E. J., . . . Vigilant, L. (2014). The genetic population structure of wild western lowland gorillas (*Gorilla gorilla gorilla*) living in continuous rain forest. *American Journal of Primatology*, *78*(9), 868–878. https://doi.org/10.1002/ajp.22274

Gatti, S., Levréro, F., Ménard, N., & Gautierhion, A. (2004). Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoué, Republic of Congo. *American Journal of Primatology*, *63*(3), 111–123. https://doi.org/10.1002/ajp.20045

Genton, C., Cristescu, R., Gatti, S., Levréro, F., Bigot, E., Motsch, P., . . . Ménard, N. (2017). Using demographic characteristics of populations to detect spatial fragmentation following suspected ebola outbreaks in great apes. *American Journal of Physical Anthropology*, *164*, 3–10. https://doi.org/10.1002/ajpa.23275

Granjon, A. C., Rowney, C., Vigilant, L., & Langergraber, K. E. (2017). Evaluating genetic capture-recapture using a chimpanzee population of known size. *Journal of Wildlife Management*, *81*(2), 279–288. https://doi.org/10.1002/jwmg.21190

Gruber, T., & Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. *Evolutionary Anthropology*, *25*(5), 239–252. https://doi.org/10.1002/evan.21501

Guschanski, K., Caillaud, D., Robbins, M. M., & Vigilant, L. (2008). Females shape the genetic structure of a gorilla population. *Current Biology*, *18*, 1809–1814. https://doi.org/10.1016/j.cub.2008.10.031

Guschanski, K., Vigilant, L., Mcneilage, A., Gray, M., Kagoda, E., & Robbins, M. M. (2009). Counting elusive animals: Comparing field and genetic census of the entire mountain gorilla population of Bwindi Impenetrable National Park, Uganda. *Biological Conservation*, *142*, 290–300. https://doi.org/10.1016/j.biocon.2008.10.024

Harcourt, A. H., & Stewart, K. J. (2007a). *Gorilla society: Conflict, compromise, and cooperation between the sexes*. Chicago: University of Chicago Press.

Harcourt, A. H., & Stewart, K. J. (2007b). Gorilla society: What we know and don't know. *Evolutionary Anthropology*, *16*(4), 147–158. https://doi.org/10.1002/evan.20142

Head, J. S., Boesch, C., Robbins, M. M., Rabanal, L. I., Makaga, L., & Kühl, H. S. (2013). Effective sociodemographic population assessment of elusive species in ecology and conservation management. *Ecology and Evolution*, *3*(9), 2903–2916. https://doi.org/10.1002/ece3.670

Jeffery, K. J., Abernethy, K. A., Tutin, C. E. G., Anthony, N. A., & Bruford, M. W. (2007). Who killed Porthos? Genetic tracking of a gorilla death. *Integrative Zoology*, *2*(2), 111–119. https://doi.org/10.1111/j.1749–4877.2007.00050.x

Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, *16*(5), 1099–1106. https://doi.org/10.1111/j.1365–294X. 2007.03089.x

Kappeler, P. M., & Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, *23*(4), 707–740. https://doi.org/10.1023/A:1015520830318

Kunz, T. H., & Lumsden, L. F., (2005). Ecology of cavity and foliage roosting bats. In T. H. Kunz, & B. Fenton (Eds.), *Bat ecology* (pp. 3–69). Chicago: University of Chicago Press.

L'Italien, L., Weladji, R. B., Holand, Ø., Røed, K. H., Nieminen, M., & Côté, S. D. (2012). Mating group size and stability in reindeer rangifer tarandus: The effects of male characteristics, sex ratio and male age structure. *Ethology*, *118*(8), 783–792. https://doi.org/10.1111/j.1439–0310.2012.02073.x

Lampa, S., Henle, K., Klenke, R., Hoehn, M., & Gruber, B. (2013). How to overcome genotyping errors in non-invasive genetic mark-recapture population size estimation—A review of available methods illustrated by a case study. *Journal of Wildlife Management*, *77*(8), 1490–1511. https://doi.org/10.1002/jwmg.604

Langergraber, K. E., Mitani, J. C., Watts, D. P., & Vigilant, L. (2013). Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(6), 861–873. https://doi.org/10.1007/s00265-013-1509-6

Langergraber, K. E., Rowney, C., Schubert, G., Crockford, C., Hobaiter, C., Wittig, R., . . . Vigilant, L. (2014). How old are chimpanzee communities? Time to the most recent common ancestor of the Y-chromosome in highly patrilocal societies. *Journal of Human Evolution*, *69*, 1–7. https://doi.org/10.1016/j.jhevol.2013.12.005

Langergraber, K. E., Siedel, H., Mitani, J. C., Wrangham, R. W., Reynolds, V., Hunt, K., & Vigilant, L. (2007). The genetic signature of sex-biased migration in patrilocal chimpanzees and humans. *PLoS ONE*, *2*(10), 1–7. https://doi.org/10.1371/journal.pone.0000973

Leslie, S., Winney, B., Hellenthal, G., Davison, D., Boumertit, A., Day, T., . . . Bodmer, W. (2015). The fine-scale genetic structure of the British population. *Nature*, *519*(7543), 309–314. https://doi.org/10.1038/nature14230

Levréro, F., Gatti, S., Ménard, N., Petit, E., Caillaud, D., & Gautier-Hion, A. (2006). Living in nonbreeding groups: An alternative strategy for maturing gorillas. *American Journal of Primatology*, *68*(3), 275–291. https://doi.org/10.1002/ajp.20223

Magliocca, F., Querouil, S., & Gautier-Hion, A. (1999). Population structure and group composition of western lowland gorillas in North-Western Republic of Congos. *American Journal of Primatology*, *48*(1), 1–14. https://doi.org/10.1002/(SICI)1098-2345(1999)48:1<1::AID-AJP1>3.0.CO;2-2

McCarthy, M. S., Lester, J. D., Howe, E. J., Arandjelovic, M., Stanford, C. B., & Vigilant, L. (2015). Genetic censusing identifies an unexpectedly sizeable population of an endangered large mammal in a fragmented forest landscape. *BMC Ecology*, *15*, 1–15. https://doi.org/10.1186/s12898-015-0052-x

Miller, C. R., Joyce, P., & Waits, L. P. (2002). Assessing allelic dropout and genotype reliability using maximum likelihood. *Genetics*, *160*(1), 357–366. https://doi.org/Article

Miller, L. M., Ward, M. C., & Schultz, D. W. (2015). Using genetic markers as individual tags: A case study of a mark-recapture estimate of adult muskellunge population size. *North American Journal of Fisheries Management*, *35*(2), 210–215. https://doi.org/10.1080/02755947.2014.996688

Moore, D. L., Langergraber, K. E., & Vigilant, L. (2015). Genetic analyses suggest male philopatry and territoriality in savanna-woodland chimpanzees (*Pan troglodytes schweinfurthii*) of ugalla, Tanzania. *International Journal of Primatology*, *36*(2), 377–397. https://doi.org/10.1007/s10764-015-9830-8

Morin, P. A., Chambers, K. E., Boesch, C., & Vigilant, L. (2001). Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Molecular Ecology*, *10*(7), 1835–1844. https://doi.org/10.1046/j.0962–1083.2001.01308.x

Muñoz-Romo, M., Herrera, E. A., & Kunz, T. H. (2008). Roosting behavior and group stability of the big fruit-eating bat *Artibeus lituratus* (*Chiroptera: Phyllostomidae*). *Mammalian Biology*, *73*(3), 214–221. https://doi.org/10.1016/j.mambio.2007.05.013

Navidi, W., Arnheim, N., & Waterman, M. S. (1992). A multiple-tubes approach for accurate genotyping of very small DNA samples by using

PCR: statistical considerations. *American Journal of Human Genetics*, *50*(2), 347–359.

Nishida, T., Hiraiwa-Hasegawa, M. (1987). Chimpanzee and bonobos: Cooperative relationships among males. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, & R. W. Wrangham (Eds.), *Primate societies* (pp. 165–177). Chicago: The University of Chicago Press.

Nunn, C. L., Thrall, P. H., Stewart, K., & Harcourt, A. H. (2008). Emerging infectious diseases and animal social systems. *Evolutionary Ecology*, *22*(4), 519–543. https://doi.org/10.1007/s10682-007-9180-x

Parnell, R. J. (2002). Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology*, *56*(56), 193–206. https://doi.org/10.1002/ajp.1074

Pines, M., Chowdhury, S., Saunders, J., & Swedell, L. (2015). The rise and fall of leader males in a multi-level society: Takeovers and tenures of male hamadryas baboons. *American Journal of Primatology*, *77*(1), 44–55. https://doi.org/10.1002/ajp.22309

Pompanon, F., Bonin, A., Bellemain, E., & Taberlet, P. (2005). Genotyping errors: Causes, consequences and solutions. *Nature Reviews Genetics*, *6*(11), 847–846. https://doi.org/10.1038/nrg1707

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959. https://doi.org/10.1111/j.1471–8286.2007.01758.x

Quinlan, R. J., & Quinlan, M. B. (2007). Evolutionary ecology of human pair-bonds. *Cross-Cultural Research*, *41*(2), 149–169.

R Development Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Retrieved from http://www.r-project.org

Robbins, A. M., Gray, M., Basabose, A., Uwingeli, P., Mburanumwe, I., Kagoda, E., & Robbins, M. M. (2013). Impact of male infanticide on the social structure of mountain gorillas. *PLoS ONE*, *8*(11), 1–10. https://doi.org/10.1371/journal.pone.0078256

Robbins, A. M., Gray, M., Breuer, T., Manguette, M., Stokes, E. J., Mburanumwe, I., ... Robbins, M. M. (2016). Mothers may shape the variations in social organization among gorillas. *Royal Society Open Science*, *3*(10), 160533. https://doi.org/10.1098/rsos.160533

Robbins, M. M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour*, *132*(1), 21–47. https://doi.org/10.1163/156853995X00261

Robbins, M. M., Bermejo, M., Cipolletta, C., Magliocca, F., Parnell, R. J., & Stokes, E. (2004). Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology*, *64*(2), 145–159. https://doi.org/10.1002/ajp.20069

Robbins, M. M., Gray, M., Kagoda, E., & Robbins, A. M. (2009). Population dynamics of the Bwindi mountain gorillas. *Biological Conservation*, *142*, 2886–2895. https://doi.org/10.1016/j.biocon.2009.07.010

Roy, J., Arandjelovic, M., Bradley, B. J., Guschanski, K., Stephens, C. R., Bucknell, D., ... Vigilant, L. (2014). Recent divergences and size decreases of eastern gorilla populations. *Biology Letters*, *10*, 1–4.

Roy, J., Gray, M., Stoinski, T., Robbins, M. M., & Vigilant, L. (2014). Fine-scale genetic structure analyses suggest further male than female dispersal in mountain gorillas. *BMC Ecology*, *14*(21), 1–16. https://doi.org/10.1186/1472-6785-14-21

Roy, J., Vigilant, L., Gray, M., Wright, E., Kato, R., Kabano, P., ... Robbins, M. M. (2014). Challenges in the use of genetic mark-recapture to estimate the population size of Bwindi mountain gorillas (*Gorilla beringei beringei*). *Biological Conservation*, *180*, 249–261. https://doi.org/10.1016/j.biocon.2014.10.011

Schwartz, M. K., Luikart, G., & Waples, R. S. (2007). Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology & Evolution*, *22*(1), 25–33. https://doi.org/10.1016/j.tree.2006.08.009

Shultz, S., Opie, C., & Atkinson, Q. D. (2011). Stepwise evolution of stable sociality in primates. *Nature*, *479*(7372), 219–222. https://doi.org/10.1038/nature10601

Slatkin, M. (1993). Isolation by distance in equilibrium and non-equilibrium populations. *Evolution*, *47*(1), 264–279.

Stansbury, C. R., Ausband, D. E., Zager, P., Mack, C. M., Miller, C. R., Pennell, M. W., & Waits, L. P. (2014). A long-term population monitoring approach for a wide-ranging carnivore: Noninvasive genetic sampling of gray wolf rendezvous sites in Idaho, USA. *Journal of Wildlife Management*, *78*(6), 1040–1049. https://doi.org/10.1002/jwmg.736

Steenbeek, R., Sterck, E. H. M., de Vries, H., & van Hooff, J. A. R. A. M., (2000). Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 130–145). Cambridge: Cambridge University Press.

Stoinski, T. S., Vecellio, V., Ngaboyamahina, T., Ndagijimana, F., Rosenbaum, S., & Fawcett, K. A. (2009). Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. *Animal Behaviour*, *77*(5), 1155–1164. https://doi.org/10.1016/j.anbehav.2008.12.030

Stokes, E. J., Parnell, R. J., & Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology*, *54*, 329–339. https://doi.org/10.1007/s00265-003-0630-3

Waits, L. P., & Paetkau, D. (2005). Noninvasive genetic sampling tools for wildlife biologists: A review of applications and recommendations for accurate data collection. *Journal of Wildlife Management*, *69*(4), 1419–1433. https://doi.org/10.2193/0022-541X(2005)69[1419:NGSTFW]2.0.CO;2

Waits, L., Taberlet, P., & Luikart, G. (2001). Estimating the probability of identity among genotypesin natural populations: Cautions and guidelines. *Molecular Ecology*, *10*, 249–256.

Williamson, E. A., & Feistner, A. T. C., (2003). Habituating primates: Processes, techniques, variables and ethics. In J. M. Setchell, & D. J. Curtis (Eds.), *Field and laboratory methods in primatology: A practical guide* (pp. 25–39). Cambridge: Cambridge University Press.

Yamagiwa, J., Kahekwa, J., & Basabose, A. K. (2003). Intra-specific variation in social organization of gorillas: Implications for their social evolution. *Primates*, *44*(4), 359–369. https://doi.org/10.1007/s10329-003-0049-5

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Hagemann L, Boesch C, Robbins MM, et al. Long-term group membership and dynamics in a wild western lowland gorilla population (*Gorilla gorilla gorilla*) inferred using non-invasive genetics. *Am J Primatol*. 2018;80: e22898. https://doi.org/10.1002/ajp.22898