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From groups to communities in western lowland gorillas

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Social networks are the result of interactions between individuals at different temporal scales. Thus, sporadic intergroup encounters and individual forays play a central role in defining the dynamics of populations in social species. We assessed the rate of intergroup encounters for three western lowland gorilla (*Gorilla gorilla gorilla*) groups with daily observations over 5 years, and non-invasively genotyped a larger population over four months. Both approaches revealed a social system much more dynamic than anticipated, with non-aggressive intergroup encounters that involved social play by immature individuals, exchanges of members between groups likely modulated by kinship, and absence of infanticide evidenced by infants not fathered by the silverback of the group where they were found. This resulted in a community composed of groups that interacted frequently and not-aggressively, contrasting with the more fragmented and aggressive mountain gorilla (*G. beringei beringei*) societies. Such extended sociality can promote the sharing of behavioural and cultural traits, but might also increase the susceptibility of western lowland gorillas to infectious diseases that have decimated their populations in recent times.

1. Introduction

Understanding the processes driving the structure of animal societies is a non-trivial exercise which requires disentangling stable social networks from dynamic spatio-temporal patterns [1]. In this context, temporal demographic changes and dispersal are the major drivers of variability in social group size, but are complemented with short-term segregation/aggregation events and intergroup interactions [2]. These lead to social structures above the group level with varying degrees of complexity and dynamism. Social structure and behaviour are adaptive responses to environmental pressures, and flexibility in social organization may facilitate reactions to changing environmental conditions [3]. Information on social structure is highly relevant in wildlife ecology, conservation, and management [4]. However, highly dynamic social structures can make the interpretation of social processes and their evolutionary significance a challenging task [2].

Western lowland gorillas (WLG; *Gorilla gorilla gorilla*) offer the possibility of studying the potentially complex social structure in a great ape in areas with minimal human impact. The global population of this primate, recently

estimated at about 360 000 individuals [5], has suffered a dramatic decline mainly due to massive die-offs caused by *Ebolavirus* outbreaks, and forecasts predict further sharp declines [6]. This great ape from the lowland forests and swamps of western central Africa (see electronic supplementary material, figure S1) lives in groups generally consisting of one fully mature male (silverback) and several adult females with their offspring, or in non-breeding groups [7–9].

Compared to the better-studied mountain gorilla (*G. beringei beringei*), the structure and dynamics of social groups in WLG are poorly understood [10,11]. This bias is due to the higher mobility and lower observability of WLG, impairing simultaneous monitoring of multiple groups [12]. For this reason, most of the information of social interactions in WLG have been gathered in *bais*, which are easily monitored [7–9,14,15] but rare swampy clearings in the forest where groups commingle while feeding on grasses rich in salts [13]. These observations suggest that one of the most striking differences between the two gorilla species is in their social behaviour. While mountain gorilla group interactions are frequently aggressive, WLG groups interact non-aggressively [10]. Concordantly, infanticide is frequently observed in mountain gorillas, while it has never been reported in WLG [9,16]. Also, group takeovers by outside males do not occur in WLG [9,16,17] as opposed to mountain gorillas [18]. WLG groups have just one silverback, in contrast with the frequent multi-silverback groups of mountain gorillas, where more than 15% of the infants are not sired by the dominant male [19]. Nevertheless, *bais* are sites where gorillas spend just 1% of their time [20] and not all groups have access to them. Thus, social interactions there might not be representative of what happens hidden in the dense inaccessible forests, where resources may be more limiting. In this context, assessing the degree and extent of association between social groups at a small spatial scale and over a short time period is key to understanding spatial organization and resource use. This knowledge is needed to implement effective predictive models of infectious disease transmission at large spatial and temporal scales, to interpret evolutionary processes, and to develop suitable conservation and management strategies. This is particularly important because 77% of the WLG range falls outside protected areas, making this great ape particularly vulnerable to logging and poaching [5].

In order to shed light on the social dynamics of the western lowland gorilla, we explored intergroup interactions of three breeding groups that were habituated to the presence of observers and were monitored daily in Ngaga Forest, located in one of the last strongholds for this great ape. Here, a dense population that has not been affected by Ebola outbreaks in the last decades still thrive. Additionally, we conducted an intensive non-invasive genetic survey over a larger area to identify neighbouring groups and solitary individuals, and to investigate their relatedness. This intense monitoring allowed us to assess if interactions between members of different social units (breeding and non-breeding groups, as well as solitary individuals) were frequent, and to investigate the role of kinship on these interactions. The results revealed a surprisingly dynamic western lowland gorilla society, characterized by frequent non-aggressive intergroup interactions likely facilitated by very low rates of infanticide.

2. Methods

(a) Monitoring of focal groups

We monitored three focal groups (FG1, FG2, and FG3) of habituated western lowland gorilla in Ngaga Forest, on the southwestern boundary of Odzala-Kokoua National Park (Republic of the Congo, 0°40′ N–14°60′ E, electronic supplementary material, figure S1) from 2013 to 2017 (about 305 monitoring sessions per group and year). The home ranges of these groups overlapped and the identity of each member was well known. Expert trackers and researchers located the animals early in the morning, normally before they left the nesting site and noted their behaviour between 07.00 and 16.00 h for an average of 2 h/day per focal group (range: 1–5 h). Although the groups were successfully located on most days, detailed observations were often limited by the dense vegetation. Behavioural data were recorded by M.B. and G.I. using instantaneous scan sampling, focal individual sampling, and observations *ad libitum* [21]. We conducted instantaneous scan samples at 5 min intervals to measure the amount of time that each individual was in view, time spent feeding on fruit, feeding on other food resources, resting, involved in social interactions, or travelling. During times of intergroup encounters, we stopped all other data collection and started compiling those on the intergroup interactions. We used all-occurrence sampling of behaviours focusing on aggressive (such as fighting, chasing, fleeing, spatial avoidance, biting, beating, and displacement) and affiliative behaviours (such as embraces, touch, grooming, play, sit in contact, and social mount) [22]. We watched multiple individuals and recorded behaviours at 1 min intervals. We compiled information about encounters between the focal groups (summarized in electronic supplementary material, figure S2) or between them and other groups. Some examples of these interactions are described in electronic supplementary material, table S1. Only the encounters in which we could individually identify with certainty the participants from both groups were considered. Throughout the duration of our study the focal groups varied in size (FG1: 15–17 individuals; FG2: 15–24 individuals; FG3: 22–26 individuals) as a consequence of birth, death, and dispersal events, yet always remaining under the leadership of the same silverback male.

The accompanying electronic supplementary material, video S1 (https://www.flickr.com/gp/revillaeloy/T55d36) shows four half-minute recordings of an encounter (an event during which members of different social units maintain visual contact with one another in close proximity, usually less than 10 m) between two non-focal groups obtained using camera traps to exemplify some of the observed interactions (two-way actions between members of different social units). These were considered aggressive when consisting of or escalating into any physical harassment or threatening behaviour. The specific encounter filmed in the video lasted for 279 min during which individuals of the two groups fed and interacted non-aggressively. In particular, the video shows juveniles of the two groups playing together, occasionally under close monitoring by older individuals that tolerated their interactions. It also shows that social play could be gentle or rough. Gentle play included behaviours such as tickling, jumping, and gentle wrestling. Rough play included more rigorous and acrobatic behaviours such as play fighting, twirling, chasing, and pushing, which were often punctuated by transitional periods of low activity. In general, play sessions started when an individual first directed a playful pattern towards another and ended when the playmates stopped their activities or one of them moved away. Within social play, we distinguished between locomotor-rotational play (including play recovering an item, play run, pirouetting, sliding down) when a session was characterized by the absence of any kind of physical contact between the playmates, and play fighting

(including biting, pushing, pulling, slapping, stamping, retrieving, brusque rushing), when the participants exhibited physical contact. Nevertheless, play sessions could sometimes escalate into overt aggression when ending with screaming and/or bared teeth by one of the players as well as with an aggressive interaction (e.g. chase/flee) [22].

(b) Non-invasive sample collection

A total of 279 faecal samples were collected in Ngaga Forest between May and August 2013 (electronic supplementary material, Dataset S1). The sampling area stretched over *ca* 44 km^2 mostly covered by dense forest with closed canopy and abundant Marantaceae understory. No *bais* are present in Ngaga forest. Fresh gorilla traces were searched along trails by expert local trackers and traced back to locate night nests.

Faeces were collected from the nests and we assumed that dungs associated with different nests at a given nesting site were likely to correspond to different members of the same group. Overall, we sampled 21–25 putative groups that were identified as distinct based on distance between nesting sites (greater than 1 km) and number of nests per site (possibly informative regarding group size). Opportunistic sampling was also carried out along trails when track evidence suggested the presence of just one individual (solitary individuals are difficult to track and therefore their nests cannot be easily found). The sampled groups included only two (FG1 and FG2) out of the three focal groups subject to daily monitoring while the third one (FG3) could not be located with certainty within the study area at the time of faecal sampling. However, we cannot rule out that one of the non-focal groups sampled in the periphery of the study area corresponded to FG3.

Age class for each sample was estimated from bolus diameter for the majority of the faeces [23]. However, such categorization in the field is prone to errors. Age class was ultimately confirmed for the individuals whose genealogy could be established from relatedness analyses (see below). Silverback samples were identified based on the comparatively bigger size of nest and dung, as well as on the occurrence of whitish hairs in the nest. Latitude and longitude coordinates were recorded for each sample or nesting site using a handheld GPS. Approximately 5–10 g of each faeces was placed in tubes with silica beads and later stored at −80°C in the laboratory. All research was carried out with permission from the *Agence Nationale des Parcs Nationaux* and the *Centre National de la Recherche Scientifique et Technique* of the Republic of the Congo.

(c) DNA isolation and amplification

DNA isolation was performed using about 10 mg of faeces following the hexadecyltrimethylammonium bromide (CTAB) protocol as modified by Vallet *et al.* [24]. Extracts were eluted in TE buffer (Tris 10 mM, EDTA 1 mM, pH 8.5) and stored at −20°C. Subsequent amplifications were performed in physically isolated laboratory facilities with negative controls being routinely included at each step of the laboratory workflow to check for possible contamination. Sex was assessed by targeting a fragment of the X-Y amelogenin homologous gene as in Bradley *et al.* [25] and the SRY gene as in Di Fiore [26]. Samples were genotyped at 17 tetranucleotide autosomal microsatellite loci using fluorescently labelled primers and multiplex amplifications as in Le Gouar *et al.* [27]. Separation of PCR products was achieved by capillary electrophoresis on an ABI 3130XL sequencer (Applied Biosystems) with an internal size standard (GENESCAN-500 LIZ). Each locus was amplified between two and 12 times for each faecal sample. Consensus individual multilocus genotypes were obtained by comparing genotypes retrieved in independent reactions. While heterozygous genotypes were confirmed with at least two independent replicates, homozygous needed three to four replicates depending on the locus variability. This number of replicates was adjusted considering allelic dropout and false allele rates estimated by comparing consensus genotypes to PCR replicates [28]. This approach allows a by-locus genotyping scheme by minimizing mistyping due to false alleles and allelic dropout rates. Only individual faeces successfully genotyped at a minimum of six loci were retained for further analyses. This threshold enabled a reliable individual identification ($P(ID)sib < 0.01$, see below).

(d) Individual identification and genetic variability

Identification of faeces deposited by the same individual was carried out with GENECAP [29] and CERVUS v.3.0.7 [30]. These programs identify exact matches and estimate the probability of identity among siblings, *P(ID)sib*, a more conservative estimation of the probability that two random individuals from the population share the same genotype, *P(ID)*, by considering the presence of close relatives. Two or more samples were considered as recaptures of the same individual when their multilocus genotypes were identical at all loci typed in both samples ($\geq$6 loci; this minimum number of identical loci was chosen to obtain *P(ID)sib* values within the range recommended for non-invasive studies: $0.0001 < P(ID)sib < 0.01$ [31]). Since faecal samples are prone to genotyping errors due to false alleles and allelic dropout, they could result in slightly different genotypes for the same individual. We first used MM-DIST [32] to obtain distributions of pairwise mismatches for the empirical data and for pairs of simulated genotypes with different degrees of kinship (parent–offspring, full-siblings, and unrelated individuals). The empirical frequencies for mismatches at one or two loci were 0.004 and 0.01, respectively, yet simulated values were always orders of magnitude lower (less than 0.0001) for all kinship categories. This strongly suggested that genotyping errors could be responsible for most of the cases of mismatches at just one or two loci. The R package allelematch [33] confirmed two as the maximum number of mismatching alleles tolerated as possible genotyping errors. Consequently, genotypes differing by one or two alleles were considered recaptures of the same individual.

Samples from the same individual and collected on the same date and location were considered the same capture event and not recaptures (for example, multiple faecal samples from the same individual in a group of nests, collected assuming that they could correspond to different individuals, $n = 52$). A total of 86 faeces represented recaptures which were collected up to nine times on different dates. Once we established the final set of unique individual genotypes, population allele frequencies were calculated using GENALEX v.6.502 [34,35]. Expected (H_E) and observed (H_O) heterozygosity were computed with ARLEQUIN v.3.5.2.2 [36]. The number of alleles per locus ranged from six to 18, and average ($\pm$s.d.) H_E and H_O were 0.759 ($\pm$0.097) and 0.760 ($\pm$0.088), respectively.

(e) Social unit identification, structure, and transfer of individuals between groups

We used a hierarchical version of the network community detection algorithm Infomap [37] (http://www.mapequation.org/code.html) to identify sets of genotypes (individuals) that tended to occur together across time and space. Co-occurrence was taken as evidence of membership in the same social unit and allowed inferring the number of social groups sampled in the genetic survey. We adopted this method because it is known to outperform similar approaches in terms of recovering the optimal network topology [38]. Specifically, the social structure of our sample was explored by drawing a modular social network associated with a co-occurrence matrix connecting each individual

to the others based on the instances when they were sampled together in the same nesting site and on the same day. We ran Infomap by using the individuals (identified by the genotypes) as nodes and the co-occurrence patterns as links. In other words, we created a link between two individuals that slept in the same nesting site. We carried out 10 000 runs and chose the best network on the basis of the code length indicator [37].

This approach also allowed the identification of individuals that were associated with different groups on different dates, implying transfers between the groups. These transfers were responsible for the hierarchical modular structure found in the population. Due to the difficulties associated with genotype reconstruction from faeces (see above), we paid close attention to the genotypes of these individuals to make sure that none of them was associated with potential genotyping errors.

We estimated relatedness (r) between individual genotypes with COANCESTRY [39]. Since identical relatedness values are expected for full siblings and for parent–offspring pairs, dyadic relatedness values were complemented with genealogy reconstruction to differentiate the two possibilities using COLONY [40] (see Supplementary Methods).

(f) Distribution of relatedness values in the population

The distribution of pairwise relatedness estimates between and within sexes as well as between and within social units and across space was explored by permutation analyses (10 000 permutations) implemented in *ad hoc* Microsoft Excel macros developed by Lukas *et al.* [41] (see Supplementary Methods).

3. Results

(a) Monitoring of focal groups

During the 5 years of intense monitoring we observed gorilla focal groups on 1525 days. We registered a minimum of 34 daytime intergroup encounters involving exclusively the focal groups (lasting 30 h in total) and of which four were encounters of all three groups. In addition, we observed three encounters with non-focal groups, although the real number could be higher because these groups avoid being close to humans. Overall, the rate of intergroup encounter was 2% (34 in 1525 monitoring days) for the three focal groups. Because of the limited visibility in the dense Marantaceae understory, the observed encounters represented a gross underestimate of the total encounter rate. During these events 39 to 55 gorillas would meet with distances of less than 10 m between groups and even with direct contact between members of the different social units. We found that the frequency of encounters between pairs of groups was quite heterogeneous and some met more often than others (electronic supplementary material, figure S2). All interactions among members of different groups were non-aggressive, lasting from a few minutes to several hours, and included feeding on the same resources and social play, typically between immature individuals. In addition, we also observed social play between adults; adult females played with each other as well as with immature individuals, suggesting a high motivation to engage in such interactions (see electronic supplementary material, video S1). Interestingly, silverbacks were very tolerant towards these activities, closely monitoring the individuals involved in the interactions and staying a few metres apart, but without showing any aggressive behaviour. Social play involving members of two or three groups required a high degree of reciprocity, cooperation, and communication between play mates (for some examples of interactions see electronic supplementary material, table S1).

(b) Non-invasive genotyping

We collected a total of 279 gorilla faecal samples (electronic supplementary material, Dataset S1). Molecular sexing was successful for 277 of these and failed for the other two due to low quality DNA. Overall, 144 male and 133 female faeces were found. Of these, 254 samples were scored at a minimum of six loci and retained for downstream analyses. Among these we identified 125 different individuals and on average their genotypes (electronic supplementary material, Dataset S2) were complete for 94% of the loci. Of these individuals, 64 (51%) were males and 61 (49%) females. Allelic dropout and false allele error rates per locus ranged from 0.01 to 0.15 and 0.02 to 0.10, respectively. The *P(ID)sib* per locus ranged from 0.300 to 0.508, and reached 1.32×10^{-7} for the entire set of loci.

We used the information on genotype profiles, collection, site and date to infer putative groups. Some of the groups were located multiple times (figure 1*a*). Field (presence of white hairs in nests or faeces) and genetic (confirmed paternities) suggested the presence of 14 candidate silverbacks, 9 of which were found within putative groups (one per group). The remaining 5 plus 4 other individuals (two males and two females) were always sampled alone (on up to two different occasions: figure 1*a*).

Interestingly, six individuals appeared integrated within different putative groups at different times, complicating the definition of social units. Hence, we used a network community algorithm to identify social groups based on the frequency at which individuals were sampled together. This analysis yielded a modular structure [2], with multiple social groups and some individuals sampled alone. We identified 16 groups composed of 2 to 17 individuals (figure 1*b*). We found nine breeding groups (FG1, FG2, G3, G7, G8, G9, G10, G12, and G15) defined by parent–offspring relationships between group members, one bachelor group (a social unit mostly including immature individuals, male-biased and with no reproductively active females [7]: G13, composed of at least 10 males and one immature female), and six more non-breeding groups (G4, G5, G6, G11, G14, and G16: figure 1*c*) including adult individuals of both sexes but no offspring.

One of the groups, G9, was resampled on five occasions at different locations, but its composition was never the same (figure 1*a*). The resampling data showed a clear internal structure in the pattern of co-occurrence (figure 2). The silverback was repeatedly sampled with one immature male (one of his sons) and two adult females, whereas other adult females and immature members of the group were found with them less often. The fact that immature animals were resampled in fewer cases with their group mates suggests that they frequently spent the night separated from the social unit. The same pattern was found for all groups that were sampled on multiple occasions: the resampling probability was lower for immature individuals than for adults (0.68 versus 0.88, $Z = -2.679$, $p < 0.007$; 95% CI: 0.57–0.77 versus 0.79–0.94).

Our results indicate hierarchical modularity in the population structure, with several groups assembling into larger

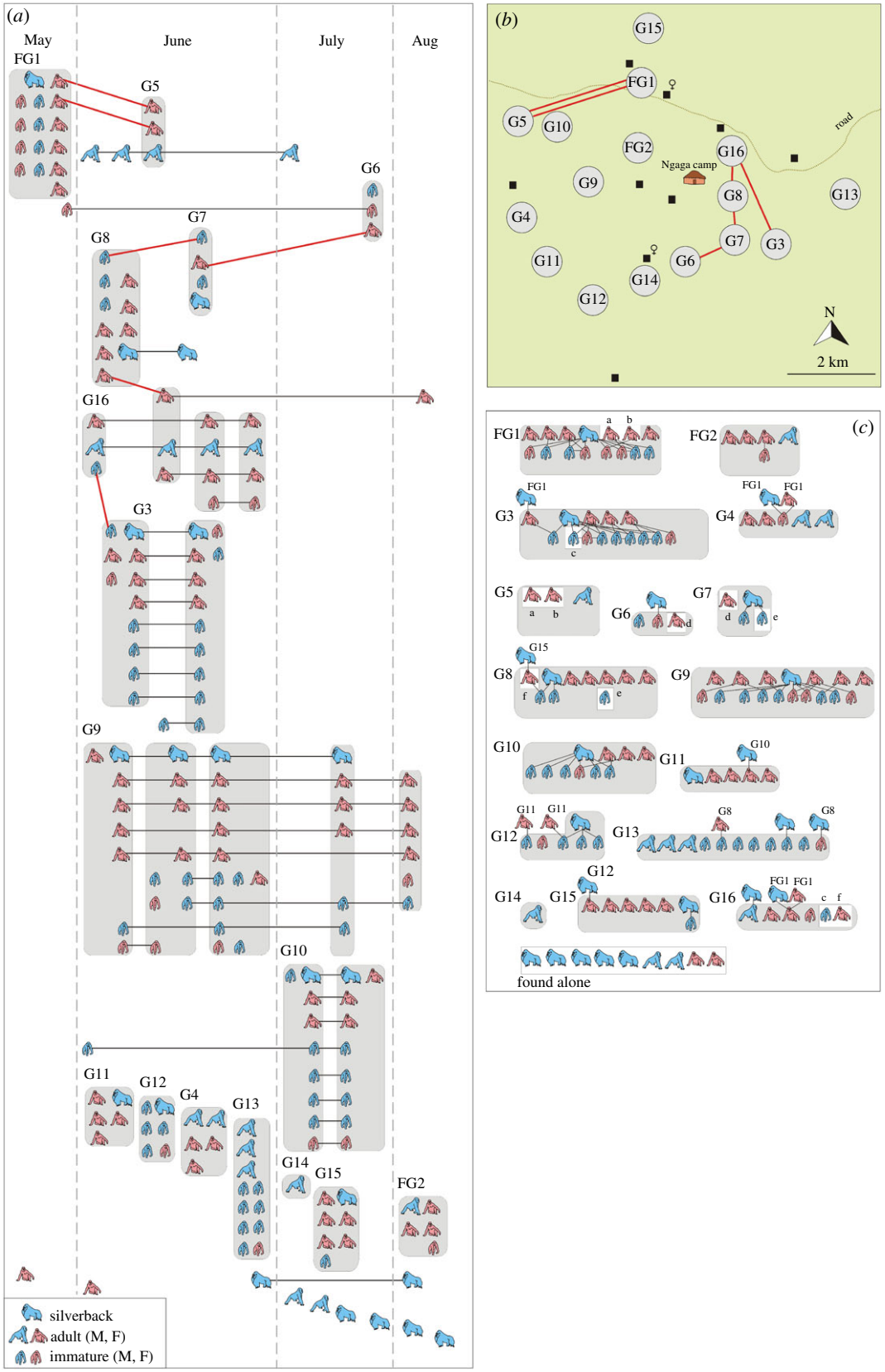

Figure 1. Non-invasive monitoring of western lowland gorilla groups through time and space. (*a*) Faeces of different individuals collected in the same place and on the same day allowed identification of putative groups (grey boxes). Recaptures on two consecutive days were collapsed into unique sampling events for graphical simplicity. Lines mark individual resampling within the same (black) or different (red) groups. For group G14, although two nests were located, only one faeces was obtained and analysed. (*b*) Relative position of the solitary gorillas (squares) and groups (group name) in the study area. Groups sampled multiple times are represented at the centroid of all the locations. Red lines indicate individual transfers between social units. Patterns of co-occurrence revealed 16 groups, with some of them (G3, G6, G7, G8, G16) joining because of individual transfers to form a 'supergroup'. (*c*) Group composition and family relationships of the 125 genetically identified individuals. Grey boxes represent groups; the white box at the bottom includes all the animals always sampled alone. Vertical and slanted lines indicate parent–offspring relationships; horizontal lines indicate full siblings. Individuals outside the boxes represent parents identified in other groups. Individuals in white insets were found in multiple groups and so appear twice in the figure (labelled with a letter to facilitate identification).

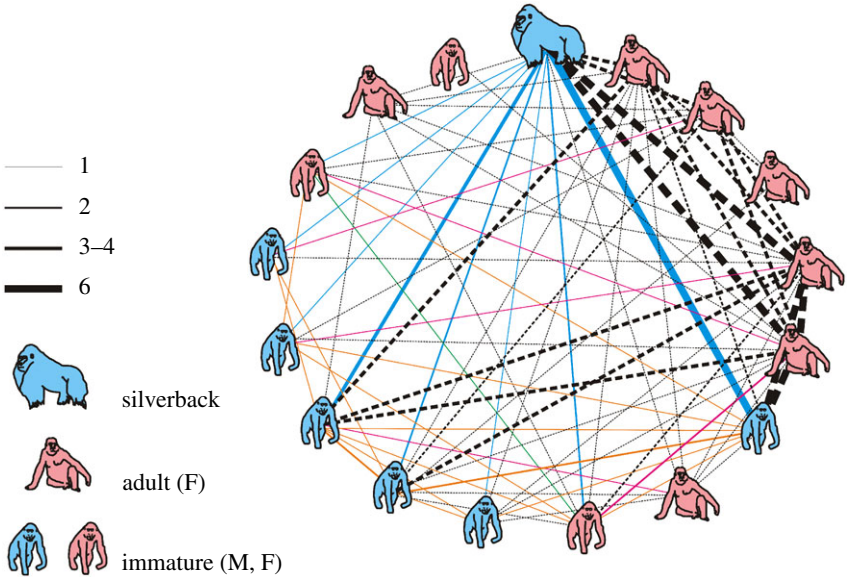

Figure 2. Internal structure and cohesiveness in group G9. The thickness of the lines connecting individuals indicates the number of times they were sampled together. The colour of the line indicates possible kinship relationships (father–offspring: blue; mother–offspring: pink; full-sib: green, half-sib: orange; unrelated: dashed black).

entities due to their dynamic composition. Despite the short sampling period, five groups (G3, G6, G7, G8, G16) joined into a 'supergroup' connected by some individuals that were sampled in different groups at different times (figure 1*a*,*b*). Two males moved from social groups composed mostly of unrelated individuals to their natal groups (from G8 and G16 to G7 and G3, respectively; figure 1*c*, electronic supplementary material, table S4). On the other hand, two females moved between groups (from G7 to G6 and G8 to G16) with silverbacks that were unrelated to them and, thus, were not their natal groups in either case. In addition, two females from group FG1 joined a roaming male maybe in an attempt to establish a separate reproductive group, G5 (figure 1*a*,*b*). The remaining groups appeared as distinct social units (figure 1*b*), but the fact that some were observed only once impaired the identification of additional intergroup transfers. In addition, a group-living female was later resampled alone, and two individuals (one female and one male) were first found alone and later integrated into groups.

The distribution of pairwise genetic relatedness r, after removing the offspring in parent-offspring pairs within social units (to exclude pre-dispersal individuals), was very similar for adult females and males, with similarly skewed distributions indicating that the majority of individuals were unrelated ($0 < r < 0.1$; electronic supplementary material, figure S3). Neither Mantel tests (electronic supplementary material, figure S4) nor permutation tests based on different distance categories ($p > 0.05$) revealed association between geographical distance and genetic relatedness in adult males or females. Nevertheless, permutation tests revealed that adult females ($n = 45$) within the same group tended to be more related than expected ($p = 0.01$) indicating that related females had settled in the same group after dispersal. However, relatedness between females and silverbacks in their own group was as expected by chance alone ($n = 35$, $p = 0.42$).

To assess the origin of males found alone, we compared them to silverbacks. Resident group-leading silverbacks ($n = 9$) were not more related to each other than to lone adult males ($n = 8$, $p = 0.37$), The males always found alone (presumably solitary individuals) were excluded as offspring of resident silverbacks. However, three of them had offspring in the bachelor group (G13) and in non-breeding groups (G6, G16: figure 1*c*).

Pedigree reconstruction confirmed that the father of pre-dispersal individuals (immatures with their parents in the same group) was usually the resident silverback (in 38 out of 41 cases, 93%; figure 1*c*). The only exceptions were three females (in groups G3 and G9) whose father could not be identified in our sample. On the other hand, mothers could be identified in the group for only 61% (23 out of 38) of the offspring sired by the silverbacks. In two cases the mothers were identified in another group within the study area (both immature individuals in group G12, with their mothers in group G11). In one more instance neither the father nor the mother could be identified within the group (G12).

4. Discussion

Our results unveil a social system much more dynamic than anticipated in WLG, with entire groups meeting and interacting, frequent exchanges of individuals between groups, and groups that varied in composition over a period of a few days implying limited cohesiveness.

Other studies have considered WLG group dynamics in the longer term, showing social units that appear, split, or disappear [42–44]. However, group dynamics here do not merely result from individual birth, death, or migration, but reflect an ever-changing society over a short time. Temporary associations to different social units in some cases involved individuals moving to groups hosting relatives. Nevertheless, this dynamic social structure went beyond family groups and the possible benefits of inclusive fitness. Some males were observed to return to their natal group; the fact that they had temporarily been in a group with unrelated individuals entails transient acceptance by social units with no kin and implies tolerance beyond kinship. Similarly, the presence in some groups of immature individuals that are not sired by the resident silverbacks, and the large mobility between social units of females with offspring may be facilitated by

the absence of infanticide [9,16]. Also, adults showed a high degree of tolerance during the encounters of focal groups. Thus, tolerance towards members of other groups may be central to the observed dynamic social structure in WLG. The distribution of pairwise genetic relatedness across sexes shows that adults were mainly unrelated suggesting that, as previous studies indicated [16] and unlike most primates, WLG exhibit potentially obligate natal dispersal by both sexes at maturity. At the same time, males in the study area were not less related than females, as would have been expected if males dispersed more frequently or over longer distances [11,45,46]. Our results also show that resident silverbacks in the study area were not more related to each other than to adult males sampled alone (presumably solitary individuals), as would be expected if the latter were mainly immigrants trying to establish new groups. Such males turned out to be systematically excluded as offspring of resident silverbacks, but some of them had offspring across the non-breeding groups. This could indicate either mating with females associated with other groups (extra-group mating) or that these solitary silverbacks had led reproductive groups in the past [15]. For females, relatedness analyses confirmed that closely related individuals dispersed together or tended to settle in groups with same-sex relatives [43,45]. On the other hand, relatedness between females and silverbacks in their own group was as expected by chance alone. All these observations suggest the high mobility of both male and female breeders in and out of the study area—in contrast with the sex-biased dispersal suggested by previous research [11,45,47]—that resulted in very low average relatedness between adults in the studied social groups.

Interestingly, genealogy reconstruction showed that some pre-dispersal individuals were not sired by the resident silverbacks (in groups G3, G9, and G12: figure 1*a*) suggesting that these gorillas may have joined the groups with their dispersing mothers. On the other hand, a relevant portion of the immature individuals sired by the silverbacks do not have their mothers within the same group, which implies that many of these adult females might have secondarily dispersed to other groups [16]. For example, two adult females in one group (G11) had their offspring in another (G12). However, our data suggest that most of the secondary dispersers may have moved outside the study area leaving offspring in their natal group, indicating high mobility of females, even after producing offspring.

In WLG, immature individuals appear to be key in facilitating social interactions between social units because they are less tightly associated with the rest of the group, are often found sleeping apart, and are frequently moving from one group to another [48]. We also observe that young individuals are less associated with the rest of the group. Previous observations have shown that immature individuals are the most likely age group to leave the safety ensured by their kin [12] and our data revealed social play encounters between groups in which immature individuals took a leading role (see electronic supplementary material, table S1).

Play fighting, a highly plastic and versatile behaviour, is widely used in animal societies to gather information on the potential role of conspecifics as competitors or social partners. In particular, this competitive/cooperative interaction serves to test the willingness to invest in a relationship and, simultaneously, to express their own willingness to accept vulnerability [49]. Play is also sensitive to the quality of group interactions, thus reflecting the very nature of social networks [50]. Thus, WLG intergroup encounters revealed strong similarities to those observed among bonobos (*Pan paniscus*) as opposed to those among the more aggressive chimpanzees (*Pan troglodytes*) [51]. While bonobos maintain a high motivation to play even during adulthood, chimpanzees progressively engage in less play fighting sessions as their age increases [22]. This study shows high motivation to play in WLG, especially in immature individuals. Gorillas may use intergroup interactions to survey potential transfer and mating opportunities. Relatively few studies have examined how factors such as interactions within and between groups or individual temperament mediate aggression and play.

There is a growing body of evidence showing how association patterns in social species are non-random. For instance, the interplay of shared space use and genetic relatedness shape association patterns in giraffe (*Giraffa camelopardalis*) social cliques [52], while female–male relationships in Guinea baboon (*Papio papio*) pairs seem to be driven by friendship beyond the sexual context [53]. For this same species, high reciprocal male tolerance is not bound by genetic relatedness [54], resulting in a complex multilevel society [55]. Among great apes, male tolerance for non-kin is well-known in notoriously peaceful bonobos [56] and was observed even among the much more aggressive chimpanzees exchanging mating tolerance for support in conflicts [57], but this behaviour has not been previously described in gorillas.

Hence, WLG are likely organized into a multilevel society as found in other gregarious animals [2], primates included [58], where groups coalescence and breakup frequently. The observed hierarchical modularity may be facilitated by the large population density in the study area (among the highest for this taxon) and the presence of spatially aggregated resources such as fruiting trees. Even though clumped resources are generally known to promote stronger territoriality and intergroup aggressiveness in some animal societies [59], they appear to be associated with tolerance in gorillas. Consistent with this view, a previous study in Lossi Sanctuary (electronic supplementary material, figure S1) [48] found that most intergroup encounters at fruiting trees involved tolerance (64%) rather than aggression (21%) or avoidance (14%).

Our findings show novel intergroup interactions of high complexity underlying a hierarchical and modular social organization dominated by fluid (e.g. many weak and only a few strong) interindividual associations as opposed to both ephemeral aggregations (e.g. a flock of birds) and stable animal societies (e.g. a pride of lions) [2]. The modular social structure emerging in this study could facilitate sharing and transmission of information (including that on kinship), or increase the potential for cultural transference [60]. Nevertheless, these same intergroup interactions in WLG may also play a major role in spreading infectious diseases [61–63]. Pathogens with high transmission potential such as *Ebolavirus* can easily travel between social units, with group-living animals being more exposed than solitary ones [47,64]. Social behaviour may thus have greatly contributed to the massive impact of past Ebola outbreaks [65,66] that have resulted in an increase of the threat level for the species, raising major conservation concerns about population declines in the

future [5,6,65]. Understanding group dynamics in social species is of utmost importance when coming to model the transmission of pathogens such as *Ebolavirus* [67,68]. However, since the high mortality imposed by outbreaks is likely to select against this social behaviour, its persistence in WLG implies that either such massive die-offs may have been rare in the past, or that the associated benefits outweigh the disadvantages. In any case, the peculiar social behaviour of western lowland gorillas is an outcome of its evolutionary history and will definitively impact its fate.

Data accessibility. The datasets supporting this study, including the geographic coordinates of faecal samples (Dataset S1) and the consensus genotypes (Dataset S2), have been uploaded as part of the electronic supplementary material and are available in the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.97kg689 [69].

Authors' contributions. M.B. and C.V. conceived the study; J.D.R.-T., G.I., G.M.-V., and M.B. collected field data; G.F., D.V., and S.D. analysed the molecular data; G.F., P.J.L.G., R.B.-M., E.R., and N.M. performed the statistical analyses; G.F. wrote the first draft of the manuscript; all authors contributed to discussions, review, and editing.

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