

Females Shape the Genetic Structure of a Gorilla Population

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Summary

Dispersal, one of the key life-history features of a species, influences gene flow and, consequently, the genetic structuring of populations. Landscape characteristics such as rivers, mountains, or habitat fragmentation affect dispersal and result in broad-scale genetic structuring of various mammalian species [1–5]. However, less attention has been paid to studying how dispersal is influenced by finer-scale microgeographic variation in a continuous habitat. Here we investigate the genetic structure of a closed population of ~300 endangered mountain gorillas living in multiple groups in a small (331 km²) forest in southwestern Uganda. In a species in which both sexes routinely disperse, population genetic structure in females was influenced by distance, altitude, and plant community composition, whereas males were not geographically structured. The effect of distance fits the observed tendency of females to transfer to neighboring groups, whereas the effects of altitude and vegetation reflect the changing species composition of locally available food resources. These results suggest that individual dietary preferences are important even in a highly mobile species living amid abundant food, and we propose that preference for natal habitats will influence dispersal decisions in many other vertebrate taxa.

Results and Discussion

We genotyped one of the two remaining mountain gorilla (*Gorilla beringei beringei*) populations by collecting fecal samples from night nests of social groups and solitary silverbacks during the 2006 census in Bwindi Impenetrable National Park, Uganda. We extracted DNA and obtained genotypes from 257 of the estimated 302 individuals [6], representing 27 of the 28 social groups and 10 solitary silverbacks. Gorilla groups ranged in size from 3 to 27 individuals, containing 1–9 adult males and 1–9 adult females. In the field, the approximate age of the individuals was assessed on the basis of the dung bolus size [7], and individuals were classified as “adults” as described in the [Experimental Procedures](#). We determined the sex of individuals by genotyping an X-Y homologous locus [8] and obtained their autosomal genotypes at 16 microsatellite loci [9, 10]. To avoid biases from including young, predispersed individuals (infants and juveniles), we limited our analysis to adult, potentially postdispersed individuals. Genotyping success did not differ between adult males

($n = 82$, data on average 89.8% complete) and adult females ($n = 98$, data on average 90.1% complete).

Genetic Structure Analysis

Using a Bayesian clustering approach that does not take the origin of samples into account (STRUCTURE version 2.1 [11]), we detected three clusters in the Bwindi gorilla population (number of individuals = 180). These genetic clusters were geographically organized. One was predominantly found in the western part of the forest, one was situated in the center of the park, and the third and smallest cluster was located in the eastern part of the park (Figure 1). These results were corroborated by the use of BAPS 5.1 [12, 13], a clustering software that also utilizes a Bayesian approach and includes geographic coordinates into the model (Figure S2, available online). Groups in the western cluster occupied the area of lowest altitude, whereas groups from central and eastern clusters were located at significantly higher altitudes (independent sample t test, equal variance not assumed, $t = -6.72$, $df = 31.6$, $p < 0.001$).

Effects of Distance, Altitude, and Vegetation

To more closely examine the relationship between the landscape and the genetic structure suggested by the clustering analyses, we next compared genetic distances between social groups with various measures of differences in landscape features. We used three data sets: adults of both sexes, only females, and only males. Using Mantel tests [14], we correlated genetic distances, measured as F_{ST} [15], with straight-line geographic distances between the nest sites of different gorilla groups. We found significant isolation by distance for the data sets containing adults of both sexes and only females, but no correlation between genetic and geographic distance for males (Table 1). We then examined whether differences in altitude between group nesting sites were correlated with genetic distances. Here again we found significant correlation for the complete data set and the female data set, but no correlation for males (Table 1). The sample size for males (number of social groups with at least two males, $n = 13$) was smaller than for females ($n = 26$), but additional analyses showed that the observed pattern could not be explained by lower statistical power in the male data set (see [Supplemental Data](#)).

Despite its small size, Bwindi Impenetrable National Park harbors a variety of very diverse habitats, characterized by differing mean temperature, rainfall, and vegetation, as the result of differences in altitude [16]. Therefore, vegetation data were collected via a stratified sampling method in five areas covering in total 84 km² of the 250 km² portion of the park occupied by gorillas (Figure S3). We extrapolated the abundance of 355 sampled plant taxa to the nest-site locations of gorilla groups by using multivariate adaptive regression splines (MARS) [17, 18]. In order to quantify the distance between each pair of extrapolated plant communities, we computed pairwise I_{ST} coefficients (I_{ST} is a parameter that expresses community differentiation among sites from species identity and abundance) [19]. We obtained two sets of three distance matrices for the vegetation data. The first set included all herb, all shrub, and all tree taxa, whereas the second set included only herb,

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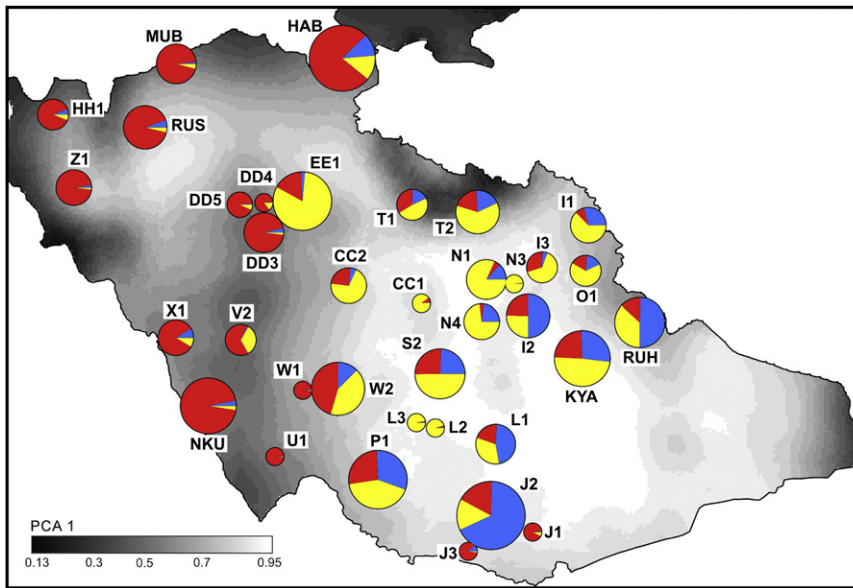


Figure 1. Sampling Locations of Social Groups and Solitary Silverbacks in Bwindi Impenetrable National Park, Uganda

Gorilla groups and solitary silverbacks are represented by circles with the size corresponding to group size. The colors of the circles represent the proportion of the group's or individual's genome attributed to one of the three genetic clusters inferred with STRUCTURE. The background represents the plant community composition in the park, and similar shadings of gray represent areas with similar vegetation compositions. The vegetation data were extrapolated for each point of the map with MARS (see Experimental Procedures). The map displays the coordinates of each point on the first axis of a principal component analysis (PCA) of the extrapolated abundance of 355 plant taxa. Not depicted is the northern sector of the park, where gorillas do not range.

shrub, and tree taxa known to be consumed by gorillas [20] (Table 1). Again, we applied simple Mantel tests to test for correlations between genetic distances and differences in plant communities. We found that for males there was no significant correlation between any of the vegetation variables and genetic distances. However, for adults of both sexes, each vegetation data set correlated significantly with genetic distances. Similarly, for females, all vegetation data sets except shrubs and shrubs that are consumed by gorillas correlated significantly with genetic distances (Table 1).

Distance, altitude, and composition of plant communities thus closely correspond to female population genetic structure. Furthermore, geographic distance, differences in altitude, and differences in the composition of plant communities were strongly collinear with one another (variance inflation factors ≥ 4.7 , max = 30.2) as a consequence of the forest geography. Bwindi Impenetrable National Park is elongated from east to west, exhibiting an altitudinal cline in the same direction. Because altitude and associated differences in temperature and rainfall are the strongest factors affecting vegetation, the differences in plant community composition also increase along the east-west axis. Thus, groups that are furthest apart from one another geographically also show the

greatest difference in altitude and in plant communities. Consequently, it was impossible to disentangle the effects of geographic distances, altitude, and plant community differences on genetic distances in the Bwindi gorilla population.

To refine our understanding of the separate effects of geographic distance and altitude upon genetic distance, we conducted a similar analysis with published data on western gorillas (*Gorilla gorilla diehli*) in the mountainous Cross River region [2]. This analysis relied on samples that were collected from seven isolated forest fragments and genotyped at 11 microsatellite loci. Altitude differences ranged from 61 to 1503 m, and geographic distances ranged from 15.5 to 89.1 km (Table 2). Although vegetation data are not available, plant community composition is expected to vary with altitude. In this region, geographic distances and altitude differences are not correlated with one another ($p = 0.286$). We found that both geographic distances and altitude differences were marginally correlated with genetic distances in a data set composed of 71 male and female Cross River gorillas (Table 2). Although many factors including severe forest fragmentation may influence the genetic differentiation between these local populations, our analysis suggests that both distance and altitude play an independent role.

Table 1. Correlation of Geographic Distance and Altitude and Vegetation Differences with Genetic Distances

	Adults Both Sexes (n = 27)	Females Only (n = 26)	Males Only (n = 13)
Log straight-line distance	$\rho = 0.40, p < 0.001^*$	$\rho = 0.45, p < 0.001^*$	$\rho = 0.04, p = 0.815$
Altitude difference (m)	$\rho = 0.23, p = 0.037^*$	$\rho = 0.30, p = 0.002^*$	$\rho = -0.04, p = 0.806$
Herbs	$\rho = 0.35, p < 0.001^*$	$\rho = 0.39, p = 0.002^*$	$\rho = 0.06, p = 0.717$
Shrubs	$\rho = 0.28, p = 0.021^*$	$\rho = 0.17, p = 0.135$	$\rho = 0.26, p = 0.202$
Trees	$\rho = 0.31, p = 0.004^*$	$\rho = 0.36, p = 0.002^*$	$\rho = 0.28, p = 0.124$
Herbs consumed ^a	$\rho = 0.35, p = 0.003^*$	$\rho = 0.40, p < 0.001^*$	$\rho = -0.12, p = 0.568$
Shrubs consumed ^a	$\rho = 0.25, p = 0.03^*$	$\rho = 0.21, p = 0.067$	$\rho = 0.26, p = 0.117$
Trees consumed ^a	$\rho = 0.34, p = 0.002^*$	$\rho = 0.36, p < 0.001^*$	$\rho = 0.32, p = 0.058$

n: number of social groups used for the analysis, each containing at least two individuals. p values were obtained after 1000 permutations; * indicates significant p values. Mantel tests using Spearman rank correlation between standardized genetic distances measured as $F_{ST}/1 - F_{ST}$ as response variable and log-transformed geographic distances, altitude, and plant community differences as predictor variables, respectively. Three different data sets for the response variable were tested: adult individuals of both sexes as well as females and males separately.

^aThese data sets contain only plant species that are known to be eaten by gorillas [20].

Table 2. Genetic, Geographic, and Altitude Differences of the Cross River Gorilla Population

$F_{ST}/(1 - F_{ST})$	UM	TS	BE	KM	MM	MN
Afi Mountain (AM)	0.050	0.134	0.166	0.320	0.117	0.138
Upper Mbulu (UM)		0.127	0.133	0.170	0.064	0.119
Takamanda South (TS)			0.174	0.245	0.084	0.117
Boshi Extension (BE)				0.257	0.101	0.165
Kagwene Mountain (KM)					0.262	0.229
Mbe Mountains (MM)						0.096
Mone North (MN)						
Log straight line distance						
Afi Mountain (AM)	4.828	4.752	4.571	4.950	4.190	4.872
Upper Mbulu (UM)		4.501	4.571	4.341	4.737	4.369
Takamanda South (TS)			4.660	4.666	4.612	4.336
Boshi Extension (BE)				4.767	4.494	4.731
Kagwene Mountain (KM)					4.880	4.436
Mbe Mountains (MM)						4.775
Mone North (MN)						
Altitude differences (m)						
Afi Mountain (AM)	428	474	130	1029	151	90
Upper Mbulu (UM)		902	298	601	579	518
Takamanda South (TS)			604	1503	323	384
Boshi Extension (BE)				899	281	220
Kagwene Mountain (KM)					1180	1119
Mbe Mountains (MM)						61
Mone North (MN)						

rho=0.29
p=0.072

rho=0.70
p=0.052

rho=0.18
p=0.286

Genetic distances are as published in [2], and geographic and altitude differences were calculated in ArcGIS v9.0. Correlation coefficient rho and corresponding p values were calculated with the Mantel test.

Female Dispersal Influences Genetic Structure

Our results suggest that Bwindi gorillas are genetically and geographically structured as a result of nonrandom movement by females. It is surprising to find a sex-specific signal in a species in which both sexes routinely disperse. Although some males leave their natal group to become solitary, and may travel long distances [21], females transfer directly to a neighboring group during intergroup encounters. However, the high frequency of female secondary dispersal (46% in the Virunga population and up to five dispersals per individual [22]) may be expected to result in a lack of geographic structure. Furthermore, the continuity of the habitat as well as the continuous distribution of gorilla groups suggests that the genetic structure is not driven by the presence of obvious barriers or unfavorable habitats.

Because geographic distances, altitude differences, and changes in plant communities are highly correlated in Bwindi, one interpretation of the observed genetic structure is that it simply reflects isolation by (geographic) distance. However, analysis of the Cross River gorilla population, in which both geographic distance and altitude are *independently* correlated with genetic distances, reveals that factors beyond geographic distance shape the genetic structure. We suggest that in Bwindi, altitude and concomitant changes in vegetation play an important role in driving female genetic structure. An evaluation of the distribution and abundance of important gorilla foods in two habitats in Bwindi, one at high altitude (2100–2500 m above sea level [ASL]) and one at low altitude (1450–1800 m ASL) [23] found that whereas the low-altitude habitat contained much more fruit, the high-altitude habitat had almost double the abundance of important gorilla herbs at any month of the year. Furthermore, although there

was high overlap in foods eaten by the gorillas at both locations, many important gorilla foods were found at only one of the locations (50%–54.5% of important gorilla foods found at only the high- or only the low-altitude site [16, 20]). The existence of such habitat diversity provides a framework for habitat choice. We suggest that in Bwindi, when facing a dispersal decision, females prefer to transfer to groups that range within their ecological cluster, characterized by similar vegetation. Given the high degree of home-range overlap between groups (36%–98% of annual home-range overlap [23]) and frequent intergroup encounters (0.78 per month [24]), it is plausible that females gain knowledge about the ranging of neighboring groups prior to their dispersal. The observed genetic structure would thus arise because female dispersal rates are greater within ecological clusters than between them.

Our hypothesis of the importance of natal habitat experiences on female dispersal decisions does not contradict previous studies that proposed that factors such as the quality and number of males in the new group influence female dispersal [25, 26]. However, the apparent abundance of food in the mountain gorilla habitat has precluded researchers from considering food availability as an important factor for female choice of group of residence. Furthermore, our results are in line with the general primate socioecological model, which predicts that females, driven by the fundamental energetic demands of reproduction, will adopt space use that maximizes their access to food resources [27].

Males Lack Geographic Structure

We found no association of geographic and genetic distance in males (Supplemental Data). This suggests that the distance

of male dispersal is large enough to eliminate a geographic signal, consistent with the results of a recent study of west-ern-lowland gorillas [28]. According to the socioecological model, food distribution will not drive male mountain gorillas' dispersal decisions as strongly as those of females, because male space use is most likely determined by the distribution of females, attracting them to the areas in which groups with high number of females range [29]. Future studies aimed at tracking individuals through space and time will help to uncover factors influencing male movement and provide evidence for the basis of their dispersal decisions.

Habitat Use

If habitat use and dispersal by gorillas are influenced by their habitat preferences, as suggested here, what is the potential for population growth and expansion of the Bwindi gorilla population? Two peripheral areas of the park have not been used by gorillas for some decades [7, 30]. One is characterized by bamboo that does not occur anywhere else in the forest. The other is situated at the lowest altitude range. Although many factors, including high levels of human disturbance, can explain the absence of gorillas in these areas [7], group feeding traditions [20] and unfamiliarity with available food resources may hinder gorillas from recolonizing these regions (Supplemental Data). Comprehensive phenological studies will help to evaluate the suitability of these areas as gorilla habitat.

In gorillas and other taxa, the natural recolonization of areas abandoned because of past hunting pressure or epidemics might be considerably slowed by habitat preferences if, as is often the case, vegetation or other important environmental factors are spatially structured. Furthermore, habitat connectivity, permeability, and attractiveness may be evaluated on the basis of natal experience and affect dispersal routes and distances. A recent study on mouse lemurs suggested that dispersal occurs along corridors of preferred habitats, resulting in a genetically structured population [31]. It follows that for effective gene flow to occur, it is not only necessary to have connecting habitats but also connecting habitats of the preferred type. Thus, not only deforestation but selective destruction of specific habitats can substantially influence a species' gene flow, making it susceptible to extinction. Our findings are also valuable when considering the feasibility of reintroduction projects by underlining the importance of familiarity with habitat and natal experience with choice of food species. In total, habitat preferences arising out of predispersal experiences may be important for evaluation of habitat connectivity and recolonization potential, assessment of the growth potential of threatened populations, and the design of species management plans.

The influence of landscape features on genetic structure has been shown for many vertebrate species [32–34]. However, the role of cryptic landscape differences in continuous habitats has rarely been assessed. Our study demonstrates that genetic structure can be effectively detected on a small geographic scale and that differences in dispersal distances and behavior will leave a detectable genetic signal, even in a species in which both sexes disperse. Our results further suggest that altitude-induced differences in plant communities influence gene flow in a continuously distributed species with a diverse diet. The suggested role of natal habitat preferences on dispersal decisions in female mountain gorillas fits with a growing body of work in a range of vertebrate taxa, demonstrating that early experiences influence dispersal

behavior (coyotes [35], red-tailed hawks [36], squirrels [37], and wolves [38]; see also [39, 40]). Our study of the effect of habitat upon genetic structure in one of the few mammals exhibiting routine dispersal by both sexes complements recent work on chimpanzees. Male chimpanzees are philopatric, but their space use is influenced by habitat familiarity mediated through maternal ranging patterns [41]. Our results generally suggest that preferences for familiar habitat may play an underestimated role in determining dispersal decisions, whatever the dispersing sex. Such an inference fits the predictions of simulation studies that show how environmental gradients in continuous habitats promote the emergence of genetic structure and eventual divergence [42], a process likely to be common to all biological systems that inhabit clinal environments, including microorganisms, plants, and animals.

Experimental Procedures

Study Site and Sample Collection

Bwindi Impenetrable National Park is an isolated montane forest in southwestern Uganda and covers an area of 331 km². The landscape is characterized by steep hills and narrow valleys, with altitude ranging from 1160 m ASL in the west to 2607 m ASL in the east. Fecal samples were collected from the entire population of Bwindi mountain gorillas during the census of this population in 2006 (Supplemental Data). A more detailed description of gorilla group tracking and sample collection is given in [6]. Approximate age and sex estimates were undertaken in the field through dung measurements, allowing the discrimination of adult and immature individuals. Samples with dung diameter bigger than 5.5 cm were considered to represent adult individuals [7].

Laboratory Procedure and Basic Genetic Analyses

After quantifying the DNA content in 421 samples [43] and discarding 37 samples with very low DNA quantity, we attempted to genotype 384 extracts, ranging in DNA concentration from 0.5 to 4430 pg/ μ l, at 16 micro-satellite loci [6]. To quickly obtain reliable genotypes, we established a two-step multiplexing approach [44] that increased the speed, sensitivity, and accuracy of the genotyping. We determined the sex of the sample via the amelogenin assay [8]. Polymerase chain reaction (PCR) products were resolved with ABI 3130XL automated sequencer and analyzed with GeneMapper v3.7 (Applied Biosystems). We obtained genotypes from 257 of the estimated total of 302 individuals [6], and the genotypes were on average 89.7% complete (Supplemental Data).

A single locus (D3s2459) was found to deviate significantly from Hardy-Weinberg equilibrium after Bonferroni correction for multiple testing. Because this locus had the highest rate of allelic dropout and the highest number of alleles, we manually eliminated all homozygotes, conservatively assuming that any one of them could have resulted from allelic dropout. Overall, the microsatellite loci used were polymorphic, with an average of 6.1 alleles and an average observed heterozygosity of 0.68, after excluding the D3s2459 locus. The test for global heterozygote deficiency, using GENEPOP 4.0 [45], did not reveal any deviation from Hardy-Weinberg equilibrium ($p = 0.7265$). The test for genotypic linkage disequilibrium was performed with the same software for 120 pairwise comparisons between loci. After applying sequential Bonferroni correction [46], only one dyad (loci D5s1457 and D5s1470) significantly deviated from expectations ($p < 0.001$). Although these loci are located on the same chromosome in humans and chimpanzees, they are separated by more than 8 million base pairs (<http://genome.ucsc.edu>), which makes linkage unlikely.

Analysis of Population Structure

We applied a Bayesian approach implemented in STRUCTURE version 2.1 [11] to a data set containing adult individuals of both sexes ($n = 180$) to test for the presence of genetic structure. This approach assumes linkage equilibrium of the loci tested. Because two of the loci used were significantly linked, we performed all analyses with all the loci and after excluding one of the linked loci. No qualitative differences were observed between the two test sets, and thus we report only the results from the complete test set. We assumed the model with population admixture and correlated allele frequencies [47].

We conducted 20 series of independent runs for each assumed number of clusters K between 1 and 8. We used the burn-in of 100,000 iterations and collected data for 100,000 iterations. Subsequently, we determined the optimal value of K by calculating ΔK [48], a measure of second-order rate of change in the likelihood of K . We also carried out a clustering analysis with the software BAPS 5.1 [12, 13] and compared the cluster assignments of individuals between STRUCTURE and BAPS (Supplemental Data). We also calculated the informativeness of the 16 microsatellite loci (Table S3) as their ability to assign individuals to the clusters inferred by STRUCTURE, measured as locus-specific F_{ST} in Genepop version 4.0 [45].

Pairwise F_{ST} values were estimated between social groups in ARLEQUIN version 3.1 [49]. We subdivided the full data set into adult females ($n = 98$) and adult males ($n = 82$) and performed the calculations with full data set as well as by analyzing males and females separately. Only groups containing two or more individuals were used. We calculated F_{ST} for 27 groups in the data set containing adults of both sexes (number of individuals per group = 2 to 15), 26 for the data set with only females (number of individuals per group = 2 to 9), and 13 for the male data set (number of individuals per group = 2 to 9). We used F_{ST} instead of R_{ST} because the migration rate in our case is much higher than the mutation rate. In this situation, F_{ST} values have lower variance and perform better than R_{ST} [50, 51].

To assign geographic location, for each gorilla social unit (groups or solitary silverbacks) we selected the first nest site found during the census. By doing that, we aimed to minimize the effect of possible disturbance of gorillas as a result of the presence of the census teams. We tested for a correlation between standardized genetic distances and log-transformed geographic distances [52] with the Mantel test [14] in a program written by R. Mundry (Supplemental Data). We used 1000 permutations to assess the significance. We also performed Mantel tests between genetic distances and altitude differences as well as differences in plant community composition.

Vegetation Data Collection and Analysis

Intensive vegetation sampling was carried out in five areas of the southern sector of the park (Figure S3). Data on the identity and abundance of 355 plant taxa were collected along 334 transects (200 m) located in each of the 500 × 500 m cells of a grid (see detailed methodology in [16, 53]). Plants were categorized as herbs, shrubs, and trees according to previous definitions [16]. ArcGIS v9.0 software was used to compute elevation, latitude, longitude, curvature, distance to the park border, and slope at the location of each transect. MARS [17, 18] were then applied to extrapolate the vegetation to unsampled locations within a 500 m radius around the gorilla group nest sites. The MARS model was fitted in R version 2.7 [54] by slight modification of the code available from the “mda” library in order to avoid obtaining negative fitting values. This was done by computing a generalized linear model with Poisson error that relates the MARS basis functions to the abundance data, following a procedure similar to that used by Leathwick et al. [18] to fit binary data. Pairwise distances between the extrapolated plant communities were subsequently computed by estimation of the values of the parameter I_{ST} [19].

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, Supplemental Results and Discussion, three figures, and three tables and can be found with this article online at [http://www.current-biology.com/supplemental/S0960-9822\(08\)01400-0](http://www.current-biology.com/supplemental/S0960-9822(08)01400-0).

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