# Dispersed Male Networks in Western Gorillas

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## Summary

Although kin-selection theory has been widely used
to explain the tendency of individuals to bias beneficial
behaviors towards relatives living within the same so-
cial group [1], less attention has focused on kin-biased
interactions between groups.  For animal societies in
which females emigrate, as is the case for mountain
gorillas (*Gorilla beringei beringei*), encounters be-
tween males in different groups often involve aggres-
sive displays that can escalate to physical violence
and fatal injuries [2, 3].  However, recent findings on
the little-studied western gorilla (*Gorilla gorilla*) indi-
cate that interactions between social groups occur
more frequently than they do in mountain gorillas and
are often [4, 5], although not always [5, 6], surprisingly
nonaggressive.  We investigated the pattern of genetic
relationships between individuals of different groups
and found evidence suggesting a previously unrecog-
nized "dispersed male network" social structure in
western gorillas in which the single males leading so-
cial groups were usually related to one or more nearby
males. We propose that this provides a basis for extra-
group, kin-biased behaviors and may explain the re-
ported peaceful intergroup interactions. Furthermore,
these results suggest that a patrilocal social structure,
in which males remain in their natal region and poten-
tially benefit from kin associations, is a feature unifying
African apes and humans.

## Results and Discussion

DNA was extracted from hair and fecal samples col-
lected at fresh nest sites of 12 social groups and two
lone silverbacks (total n = 65 unhabituated gorillas) near
the Mondika Research Station in the Central African
Republic and Republic of Congo [4]. Gorilla densities in
this region are estimated at 1–2/km$^2$ [7], and so these
groups, sampled from an approximately 50 km$^2$ area,
are thought to represent the majority of groups ranging
within the study site. For each sample, approximate age
and sex were determined from dung bolus size [8] and
amplification of an X-Y homologous locus [9], respec-
tively, and individual genotypes at up to ten microsatel-

lite loci were determined [10]. Results indicate that all
groups contained one silverback and 2–4 adult females.
In addition, blackbacks, reproductively active males that
have not yet developed all secondary sexual character-
istics (e.g., sagittal crest, silvering hair on back), were
present in three groups (two groups with one each and
one group with seven).

We first examined patterns of paternity within social
groups by comparing genotypes of offspring to those
of all sampled silverback and blackback males. The resi-
dent silverback of the same group as the offspring was
never excluded as the sire of 20 offspring from eight
social groups (Table 1). More specifically, for ten of the
20 offspring, the silverback was the only male not ex-
cluded by mismatches in the genotypes, and paternity
exclusion probabilities were also high (Pe > 0.95). In
the remaining ten cases, although the silverback was
not excluded and thus represents the probable sire, one
or more additional males tested were also not excluded.
In many of these cases, the ability to determine paternity
with certainty was reduced by (1) the lack of a genotype
from the mother, (2) missing information in the genotype
of the offspring, or (3) the presence of probable adult
relatives of the likely silverback sire in the same or a
nearby group (Table 1). In two groups, the offspring
attributed to the resident silverback included juveniles
(estimated ages 3–6) [11] as well as infants, indicating
that at least some silverbacks maintain group leadership
for a minimum of 3–6 years. Thus, although not all as-
signments were conclusive, the paternity results are
consistent with the resident silverback siring all group
offspring.

Genetic relationships among silverbacks from differ-
ent groups, as well as lone silverbacks, were evaluated
by using both estimates of relatedness [12] and likeli-
hood analysis [13] to conservatively identify pairs of
relatives, that is, half-siblings, full-siblings, or parent-
offspring. Twelve of the 14 silverbacks analyzed were
related to one or more other silverbacks in the area
(Figure 1). In two cases (Figure 1, N and M, and I and
O), the related silverbacks did not share an allele at
each locus and therefore could be excluded as having
a parent-offspring relationship, while for all other related
dyads the likelihood analysis could not distinguish be-
tween full- and half-siblings or between sibling and
parent-offspring pairs with confidence. Since the 14
males can be paired 91 possible ways, the 11 related
dyads identified represent a minority (12%) of male
pairs. However, the distribution of related pairs across
the study site shows an interesting pattern (Figure 1).
Immediately apparent are two clusters of related males,
a "central" cluster (B, E, H, and J) and a "southern"
cluster (C, G, Q, and P), as well as two related pairs (N
and M, and I and O). Only two males (D and F) were
unrelated to all other sampled silverbacks, and one of
these (D) was sampled at the northern periphery of the
study site. Nest site locations represent each sil-
verback's position in the study site at one point in time
and do not reflect the degree or pattern of home range

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Table 1. Paternity Results for 20 Offspring

| Offspring | Resident Silverback Excluded? | Other Adult Males Excluded? | Paternity Exclusion Probability (Pe) | Assigned Sire |
|---|---|---|---|---|
| B1 | no | yes | 0.999 | resident SB |
| B3 juv | no | yes | 0.999 | resident SB |
| D2 | no | yes | 0.998 | resident SB |
| M1[b] | no | yes | 0.960 | resident SB |
| N5 | no | yes | 0.996 | resident SB |
| N6 juv | no | yes | 0.999 | resident SB |
| N8 | no | yes | 0.999 | resident SB |
| O1 | no | yes | 0.999 | resident SB |
| O4 | no | yes | 0.995 | resident SB |
| O6 | no | yes | 0.999 | resident SB |
| J4 | no | 1 not excluded | | |
| J5 | no | 1 not excluded | | |
| M3 | no | 1 not excluded[c] | | |
| J6[a] | no | 4 not excluded | | |
| Q2 juv[a,b] | no | 4 not excluded | | |
| P8 | no | 6 not excluded[c] | | |
| P9 juv | no | 6 not excluded[c] | | |
| P12 juv[b] | no | 6 not excluded[c] | | |
| B7 juv[a,b] | no | 6 not excluded | | |
| O8[a,b] | no | 10 not excluded | | |

Letters in offspring names denote group membership (i.e., B1 and B3 are in group B). Juv = juvenile, all other offspring are infants.

[a] Genotypes completed at fewer than five loci.

[b] Genotype of mother unknown.

[c] Excluded males are blackbacks in the same group as the resident silverback.

overlap between groups. Nonetheless, the sampling area is large (approximately 50 km²) relative to home range size (15 km²; approximately 6 km × 2.5 km) [4]. Thus, nest sites at opposite ends of the study site are unlikely to represent groups with overlapping home ranges, while nest sites separated by only a few kilometers probably do represent neighboring groups. Interestingly, with the exception of one dyad (C and P), the nest sites of all related silverbacks were found within 5 km
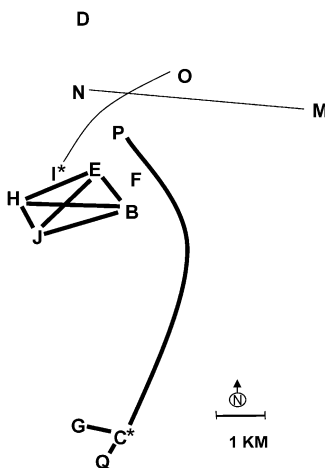


Figure 1. Relative Locations of Gorilla Nesting Sites and Related Silverbacks

All lines indicate related dyads (see text). Thin lines indicate dyads that can be excluded as father-son pairs based on allelic mismatches, while thick lines indicate that the relationship type (half-sib, full-sib, father-son) could not be distinguished. All other possible dyads have no relationship. * = lone silverback; all others are group silverbacks.

of each other (Figure 1). A matrix correlation test [14] showed a small but significant negative relationship between silverback relatedness and distance between nest sites (Kr = −138, Kendalls Tau = −0.14, n = 14, p < 0.05). When the same analysis was done comparing genotypes of the breeding females, no correlation between relatedness and distance was observed (Kr = 29, Kendalls Tau = 0.02, n = 15, p = 0.63).

Although both male and female western gorillas have been observed to emigrate from their natal group upon reaching maturity [15], our results suggest that dispersing males often do not go far and remain in the vicinity of male kin. That adult male western gorillas seem to form neighborhoods in which related males live close together is especially interesting in light of previous behavioral findings [4, 5, 16, 17] showing that intergroup encounters in western gorillas are relatively frequent (four times that of mountain gorillas [3, 4]) and often surprisingly peaceful, that is, males show no reaction to each other, even when group members comingle [4].

We believe the results are suggestive of a previously unrecognized dispersed male network social structure in western gorillas. This social structure is characterized by the presence of independent groups led by single adult silverbacks that interact with other social groups led by related silverbacks. This situation may arise as a consequence of the pattern of reproduction and dispersal in western gorillas. We have shown that the resident silverback male can monopolize paternity for several years, thus producing multiple offspring related on average at the level of half-siblings. Infant, juvenile, and adolescent developmental periods are long, lasting at least 8 years [11]. This long period of close interactions within the group provides a means for kin recognition through social familiarity [18]. Male networks may bene-

fit younger males as they attempt to attract females and form new groups since male-male aggression, which hinders acquisition and retention of females [19], should decrease when some, but not all, competitors are kin [20]. If males are successful in forming new groups, the outcome will be one or more groups led by related males ranging in the same area. The behavioral findings of frequent peaceful intergroup encounters can thus plausibly be attributed to kin-biased affiliative behaviors across groups. Direct testing of this hypothesis and rejection of alternative explanations, such as a situation in which neighbors are familiar and hence are tolerated to a greater extent than strangers [21], requires further work specifically directed toward behavioral observation and relatedness estimation of individually identified western gorilla males. Such research is only now becoming feasible due to recent progress in habituation of western gorillas.

In contrast to western gorillas, in which virtually all groups contain only one silverback male, in eastern mountain gorillas, fewer than half of the males who reach maturity in heterosexual groups emigrate, resulting in a substantial proportion (~40%) of groups with multiple silverbacks who are often related [22]. While intergroup encounters are relatively infrequent in mountain gorillas (<1 per month), the majority (74%–93%) involve aggressive male-male threat displays, such as chest beating and charging, and both dominant and subordinate silverbacks act to maintain group cohesion by herding group females [3]. Thus it seems likely that the benefits for male philopatry in mountain gorillas may occur largely within, rather than between, groups. Interestingly, the dispersed male network scenario is indirectly supported by the rare instances of peaceful intergroup interactions in mountain gorillas in which the groups involved contained possibly related males formerly resident together in one group [16].

Benefits of male kin proximity have been reported in birds, where males typically disperse less far than do females and the presence of male kin can help in establishing territories [23] and attracting mates [24]. In mammals, however, male-biased dispersal is the norm [23], and social networks of philopatric males are exceedingly rare. Notably, the social structure of western gorillas seems similar to that of chimpanzees and humans in which patrilocality has been suggested to influence kin-biased behaviors between males [25–27]. Although the degree to which the presence of male kin influences cooperative behavior within chimpanzee groups is questionable [28], it undoubtedly influences marriage and alliance patterns in humans [25]. This report of apparent dispersed male networks in gorillas means that a form of a patrilocal social structure, in which kin-biased interactions can occur within or between groups, is a common feature of African ape societies as well as human societies and has important implications for understanding the social structure of early humans.

## Experimental Procedures

### Study Site and Sample Collection

Hair (n = 2) and fecal (n = 63) samples were collected at fresh nest sites of wild, unhabituated gorillas at Mondika Research Center on

the Central African Republic and Republic of Congo border (02° 21'N, 016° 16'E) [4]. Fecal samples at each nest site were assigned to relative age class on the basis of approximate bolus diameter [8] (infant, <2 cm; juvenile, 2–4 cm; adult female or black back male, 5–6 cm; silverback, >7 cm). Identifications of silverback nests were further aided by the presence of numerous long, gray hairs. Mother-offspring pairs were identified by the presence of infant-sized and adult-sized dung in a single nest. Sample collection and storage procedures were as previously described [9]. Sampled nest sites covered an area of approximately 50 km$^2$.

### Genetic Analysis

Genomic DNA was extracted and quantified by real-time PCR as previously described [29]. DNA extracts were amplified at up to ten microsatellite loci [10] and one X-Y homologous locus for sex identification [9]. Any sample that was categorized by size as adult or silverback and typed as male was subsequently conservatively considered to be a male of reproductive age and a potential sire in paternity analysis. Genotype scoring followed stringent criteria of numerous independent replications [29], meaning homozygous genotypes were confirmed by multiple independent replications and heterozygous genotypes were confirmed by scoring each allele at least twice in two or more independent reactions.

### Statistical Analysis

Across the set of ten loci, silverback genotypes were 89% complete. Only four individuals (all offspring) out of 65 were genotyped at fewer than five loci. Average observed heterozygosity was 0.83, with an average of 6.6 alleles per locus, and no deviations from Hardy-Weinberg equilibrium were detected [30]. This suite of loci was sufficiently variable to distinguish individuals by their multilocus genotypes and the probability that two related individuals share the same genotype [31] was $1.29 \times 10^{-4}$. Similarly, the estimated average paternity exclusionary probability [30] of this set of loci was high (0.999 if mother's genotype is known, and 0.985 if neither parent is known).

Although maternity of infants could usually be inferred by nest sharing with the mother and confirmed by comparison of genotypes, juveniles build their own nests. Maternity was genetically assigned for four juveniles by comparing their genotypes with those of adult females in the same group. For each of these juveniles, only one group female shared an allele at every locus (Pe = 0.83 – 0.99) and was considered the mother. All sampled adult males in the study site (n = 23) were considered as potential sires for all offspring (n = 20). Paternity assignments were done by exclusion of males having mismatches to the offspring genotype or, when data from the mother was present, the inferred paternal component of the genotype. Individual paternity exclusion probabilities were calculated as described elsewhere [32].

Dyadic relatedness (R) was evaluated by using the estimator implemented in the program RELATEDNESS v.5.0.8 [12]. Relationships were further examined using KINSHIP [13], which evaluates likelihood ratios for primary/null hypothetical pedigree relationships. We tested two relationships (half-sibling and full-sibling) as primary hypotheses versus a null hypothesis of no relationship and evaluated significance by using 10,000 simulations. For both the RELATEDNESS and KINSHIP analyses we used allele frequencies based on all adults (n = 45), as recommended for analysis of populations containing related and unrelated individuals [13]. We conservatively considered related dyads to be those with both R values ≥0.2 and significant likelihood ratios (p < 0.05) for half- and/or full-sib primary hypotheses. The presence of allelic mismatches allowed us to exclude two related dyads as father-son pairs (N and M, and I and O; Figure 1). For all other related silverback dyads, the type of relationship (half-sib, full-sib, father-son) could not be distinguished.

The relationship between nest site distance (to the nearest 0.5 km) and relatedness (in categories at 0.05 increments) was evaluated using a nonparametric variation on the Mantel Test, a Kr permutation matrix correlation test taking into account the dependence of dyadic values [14]. Significance was evaluated by using 10,000 simulations.

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