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SPECIAL FEATURE: ORIGINAL ARTICLE

Understanding the Variability of Gorilla Social Structure

Group structure predicts variation in proximity relationships between male–female and male–infant pairs of mountain gorillas (*Gorilla beringei beringei*)

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Abstract Relationships between conspecifics are influenced by both ecological factors and the social organization they live in. Systematic variation of both—consistent with predictions derived from socioecology models—is well documented, but there is considerable variation within species and populations that is poorly understood. The mountain gorilla (*Gorilla beringei*) is unusual because, despite possessing morphology associated with male contest competition (e.g., extreme sexual dimorphism), they are regularly observed in both single-male and multimale groups. Both male–female and male–infant bonds are strong because males provide protection against infanticide and/or predation. Risk of these threats varies with social structure, which may influence the strength of social relationships among group members (including females and offspring, if females with lower infant mortality risk are less protective of infants). Here, we investigate the relationship between group structure and the strength of proximity relationships between males and females, males and infants, and females and offspring. Data come from 10 social groups containing 1–7 adult males, monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center in Volcanoes National Park, Rwanda. After controlling for group size and infant age, association strength was similar for male–female pairs across group types with both dominant and nondominant males, but male–infant relationships were strongest in single-male groups where paternity certainty was high and animals had fewer social partners to choose from. The male:female and male:infant ratios better predicted both male–female and male–infant associations than the absolute number of males, females, or infants did. The fewer the number of males per female or infant, the more both pair types associated. Dominant males in groups containing fewer males had higher eigenvector centrality (a measure of importance in a social network) than dominant males in groups with more males. Results indicate that nondominant males are an important influence on relationships between dominant males and females/infants despite their peripheral social positions, and that relationships between males and infants must be considered an important foundation of gorilla social structure.

Keywords Social plasticity · Group structure · Network centrality · Variable group composition · Association strength · Multimale groups

Introduction

Social relationships between individual conspecifics are influenced by both ecological factors (e.g., van Schaik 1983; Elgar 1986; Emlen 1994) and the structure of the social unit they reside in (e.g., Janson 1986; van Schaik 1996; Hemelrijk 1999). Socioecological models provide testable predictions about the relationships between environment, individual relationships, and properties of social structures that emerge from these individual interactions (Hinde 1976; Kappeler and van Schaik 2002). Systematic

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variation consistent with predictions derived from these models is well documented across species, and provides a rich understanding of the links among environment, relationships, and social structure (e.g., Boinski 1999; Nunn 1999; Doran and McNeilage 2001). However, there is ever-expanding evidence of considerable social plasticity within species and even populations (e.g., Lott 1991; Sterck 1999; Schradin and Pillay 2005; reviewed in Chapman and Rothman 2009), much of which remains poorly understood (e.g., Clutton-Brock and Janson 2012; Koenig et al. 2013; Kappeler et al. 2013).

Mountain gorillas (*Gorilla beringei beringei*) present an interesting paradox. Their morphology (extreme sexual dimorphism, well-developed male weaponry, small testes-to-body-size ratio) strongly suggests they evolved in a one-male, multi-female social system in which intrasexual selection on males was very strong (Schultz 1969; Leutenegger and Kelly 1977; Harvey et al. 1978; Harcourt et al. 1981; Møller 1988). Despite this, about 40 % of the social groups in central Africa's Virunga Massif contain multiple adult males (Stoinski et al. 2009a; Gray et al. 2010). In Uganda's Bwindi Impenetrable Forest, 6 of 11 habituated study groups contain more than one adult male as of the time of writing (Robbins, pers. comm.). Currently a substantial proportion of the world's mountain gorilla population resides in multimale/multifemale groups, despite their apparently long evolutionary history of a harem social system.

While groups containing two adult males were reported as far back as the 1950s (Schaller 1963), in the mid-1990s the subset of gorilla groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center underwent a substantial demographic shift. Social groups grew larger and many animals remained in their natal group long past sexual maturity, creating groups with (at their extremes) 65 individuals, 9 adult males co-resident at once, and a male:female ratio that approached 1:1 (Stoinski et al. 2009b). Mean group size has increased steadily over time, from 8.8 in 1976 to 12.5 by 2010 (Gray et al. 2013). While no satisfactory answer has yet been put forth to explain this structural shift, it created a remarkable opportunity to observe social plasticity in a species that few would have guessed were capable of more than occasionally tolerating a second, usually closely related, young adult male.

Mountain gorilla social structure is based on the male–female unit. The strongest adult bonds are between females and the male(s) in their group, while relationships between same-sex adults are weak (e.g., Harcourt 1979a, b; Watts 1994; Robbins 1996). The primary purpose of such relationships is believed to be protection against infanticide (Fossey 1984; Watts 1989; Harcourt and Greenberg 2001), and historically leopards (Fay 1995; Robbins et al. 2004; Harcourt and Stewart 2007). Males and infants also have close relationships that are best explained as paternal care (Stewart 2001; Rosenbaum et al. 2011). Once infants are old enough (~12 months) to begin moving about independently, adult males become a focal point of their social interactions (Fossey 1979; Fletcher 1994). Males are extremely tolerant of infants, support them in disputes with other group members, and young animals whose mothers die or emigrate are typically "adopted" by an adult male they follow during the day and nest with at night (Fossey 1979; 1983; Watts and Pusey 1993; Stewart 2001; Warren and William 2001; Rosenbaum et al. 2011).

Since both male–female and male–infant relationships are known to be strong, and both are best explained as protective responses to environmental threats benefitting all three parties [though benefits to males depend on paternity certainty (Trivers 1972) or indirect fitness (Hamilton 1964)], we might expect variation in the strength of these relationships to co-vary with group composition. Groups with multiple males have lower paternity certainty

Table 1 Study group compositions

Group	Data years	# Males	# Female-offspring pairs	Males:females (infants)[b]	Mean infant age	Point samples per pair
BWE	2011–12	1	3	1:3	2.33	$\bar{x} = 294$ (min $= 96$, max $= 581$)
INS	2011–12	1	2	1:2	2.63	$\bar{x} = 268$ (min $= 160$, max $= 363$)
ISA[a]	2011–12	1	3	1:3	2.61	$\bar{x} = 312$ (min $= 223$, max $= 522$)
URU	2011–12	1	2	1:2	2.38	$\bar{x} = 154$ (min $= 113$, max $= 208$)
UGE	2011–12	2	3	1:1.5	2.36	$\bar{x} = 254$ (min $= 115$, max $= 363$)
NTA	2011–12	3	2	1:0.67	1.83	$\bar{x} = 186$ (min $= 86$, max $= 300$)
KUY	2011–12	3	5	1:1.67	3.08	$\bar{x} = 256$ (min $= 100$, max $= 1096$)
BEE	2003–05	4	6	1:1.5	2.22	$\bar{x} = 314$ (min $= 76$, max $= 761$)
PAB	2011–12	5	7	1:1.4	1.85	$\bar{x} = 261$ (min $= 80$, max $= 691$)
SHI	2003–05	7	5	1:0.7	1.82	$\bar{x} = 276$ (min $= 135$, max $= 429$)

[a] Group contained an extremely peripheral second male (removed from data; see text)

[b] Females and offspring (infants) only included in dataset when both were present, so the male:female and male:infant ratios are identical

(Bradley et al. 2005; Robbins et al. 2014; Vigilant et al. 2015), a higher ratio of males to females and infants (Table 1), and lower infant mortality (Robbins et al. 2007, 2013). Lower paternity certainty might result in weaker relationships since males would have less incentive to provide protection. This might not be true if males and infants discriminated paternity as do baboons (Buchan et al. 2003) or rhesus macaques (Langos et al. 2013), but mountain gorillas do not appear to distinguish between their own and other males' young (Rosenbaum et al. 2015).

Furthermore, the presence of multiple males might dilute the value, and therefore strength, of any one relationship. In large groups, females and infants sometimes appear to squabble over favorable resting places nearest to adult males (pers. obs.), and Watts (1992) reported that females in a group with multiple males appeared to compete for proximity and social access to one of the silverbacks. If access to space near males is indeed something females and their infants compete over [presumably because it provides better protection against infanticide and predation (Watts 1992)], a higher ratio of males to females and infants might encourage stronger ties between both males and females and males and infants, since there is less competition. This assumes that all males are equally preferred social partners for females and infants, which is not the case; most prefer the dominant male to all others (Sicotte 1994; Stewart 2001; Rosenbaum et al. 2011). The overall ratio of males to females and infants is irrelevant if females and infants all want to be close to the same male, meaning that the ratio important to females and infants (dominant male to females and infants, or simply the absolute number of females/infants, since a group can only contain one dominant male) would typically be higher in multimale groups since they usually contain more females and infants (see Caillaud et al. 2014 for a demographic overview).

The goal of this paper is to describe the relationship between social organization and proximity relationships between members of the core male–female–infant triad underlying gorilla social structure. In mountain gorillas, time spent in close proximity is a primary measure of social closeness, and it is frequently used to make inferences about social relationships (e.g., Watts 1992, 1994; Nakamichi and Kato 2001; Stoinski et al. 2003). Multiple lines of empirical evidence support this inference. Maternal relatives and longer-term social partners (i.e., natal residents versus immigrants) spend more time in proximity to one another than unrelated or new social partners (Watts 1992, 1994). Avoidance of close proximity may be used to deter aggression (e.g., Robbins 1996). Initiating and maintaining close proximity is a primary post-conflict reconciliation mechanism in gorillas (Mallavarapu et al. 2006). Furthermore, proximity tolerance can be a proximate mechanism underlying fitness benefits in mammals (sea lions: Wolf and Trillmich 2008; Columbian ground squirrels: Viblanc et al. 2010).

We evaluated whether the strength of associations between males and females (M–F), males and infants (M–I), and females and their offspring (F–O) varies as a function of the number of males in a group. As in all primates, due to their altricial young, relationships between mothers and infants are the strongest social bond in any gorilla group (e.g., Altmann 1980; Fletcher 2001). We include an investigation of F–O pairs in these analyses because in multimale groups, where infant mortality risk is lower, females may be comfortable allowing infants more independence at earlier ages, weakening the bond relative to their peers in groups with one male.

In addition to traditional dyadic analyses, we used social network analyses, which provide a more holistic picture (Wey et al. 2008) and are useful for visualizing the complex variation observed in this species. Specifically, we used network methods to determine whether the importance of individual males to group structure varies with the number of males in a group by calculating eigenvector centrality (Bonacich 1987). Eigenvector centrality is an indicator of individuals' importance to network structure which takes into account both the strength of the individual's connections and the strength of their connections' connections. We also used network measures to determine whether group structure is associated with group-level measures of eigenvector centrality across age/sex classes. We predict that:

1. In all group types, ties will be strongest between F–O pairs, M–F ties will be intermediate, and M–I ties will be the weakest of the pair types evaluated.
2. In multimale groups the strength of nondominant M–F and nondominant M–I ties will weaken as the number of males increases, because females and infants have more male social partners to choose from, thereby diminishing the value of a relationship with any one male. F–O ties will also be weaker in groups with more males than groups with fewer males, since infants in such groups are better protected from infanticide and predation. However, the strength of associations for M–F and M–I pairs that contain dominant males will be the same regardless of the number of males in the group, because most females and infants prefer the dominant male to all others.
3. The absolute number of females and infants will better predict M–F and M–I association strength than (a) absolute number of males or (b) the ratios of all males: females and males: infants, because most females and infants prefer the dominant male to all others. When there are more females and infants, they have more competition for proximity to the dominant male.

4. Group-level eigenvector centrality will get progressively lower as the number of males increases, because adult males do not typically spend much time in close proximity to one another (Robbins 1996, 2001), and females and their offspring tend to cluster around males (e.g., Harcourt 1979b). This may result in more subgrouping in multimale groups, and thus such groups should have lower group centrality measures.
5. Males in single-male groups will have higher individual-level eigenvector centrality than dominant males in multimale groups, because even though females and infants in multimale groups generally prefer the dominant male, the value of a relationship with the dominant male is lower when there are other adult males present.

Methods

Site and data collection protocol

This study was conducted on the habituated mountain gorillas monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center (KRC) in Volcanoes National Park, Rwanda. The first author conducted 50-min focal animal sampling on adult males (in 2003–2004 and 2011–2012) and infants between 1 and 4 years old (in 2011–2012). Data were also extracted from the long-term KRC database records for 2003–2005 and 2011–2012. Long-term data were collected by a variety of observers on adult males, females, and infants. All observers passed animal identification tests and repeated inter-observer reliability tests. Each focal observation included instantaneous proximity point samples collected at 10-min intervals where the identification of each animal within 2 m of the focal subject was recorded.

Social groups

Data come from 4 single-male groups and 6 groups with 2 or more males (Table 1). One of the groups classified as single male ostensibly contained a second silverback that we removed from the analyses because he so rarely interacted with females and infants (9 interactions in 49 h of focal animal sampling, 8 of which were aggressive and at a distance of >20 m). He was rarely observed in visual contact with the group, was never observed copulating, and paternity data available thus far confirm he has not sired infants (Vigilant et al. 2015).

To be included in the analyses, the male(s), females, and infants must have been co-resident for ≥6 months while the infant was 1–4 years old. Each pair had ≥72 proximity point samples available (equivalent to 10 h of focal animal sampling), and most had far more (mean point samples per pair = 257.5, min = 76, max = 1096; Table 1). Insufficient data eliminated the inclusion of 8 pairs in group BEE (1 M–F, 1 M–I, 6 F–O) and 13 pairs in group SHI (6 M–F, 7 M–I) (Table 1). None of these included known parents and offspring, nor the group's dominant male. If a mother gave birth to a new infant before the infant in our analyses turned 4 (interbirth interval is ~4 years; Robbins et al. 2006), data for all pairs involving that F–O were terminated.

Age-class definitions

Adult males were defined as males ≥12 years old who resided in the social group. Adult females were females with infants 1–4 years old, and infants were the corresponding offspring, roughly following age-class definitions in Watts and Pusey (1993). Only infants >1 year old are included, to eliminate the developmental period wherein infants are totally unable to make independent social partner choices and spend nearly 100 % of their time in contact with mothers. There is a dramatic increase in the time infants spend near silverbacks and away from mothers that begins between 9 months and 1 year old (Fletcher 2001). The time infants spend in close proximity to silverbacks peaks between 2 and 3 years old (Rosenbaum et al. 2011). We included infants 1 year older and 1 year younger than this peak range to capture the variation present in relationships during this important developmental stage. Infants whose mother died or dispersed before the 4-year age cutoff were included only when the mother was co-resident.

We did not consider the sex of the infant in these analyses for three reasons. First, we have no a priori reason to expect sex differences (Rosenbaum et al., in review). Second, existing work suggests that the small sex differences observed in 1–4 year old animals would be unlikely to influence our outcome variable (e.g., Fossey 1979, Fletcher 2001; Rosenbaum et al. 2011). Third, our sample was evenly balanced between the sexes, with 19 female and 19 male infants. One of the single-male groups contained only male infants ($n = 2$), and the group with 7 males contained only female infants ($n = 5$). The other 8 groups did not have marked sex ratio imbalances.

Male dominance ranks

Adult male rank was determined using displacement patterns, as described in Stoinski et al. (2009b) and used in many publications (e.g., Robbins 1996; Bradley et al. 2005; Robbins et al. 2014). Adult males were categorized as dominant (rank 1), beta (rank 2), and gamma (rank 3).

There were rarely enough displacements to determine exact ranks beyond gamma, so all other adult males were classified as subordinates and assigned a rank of 4. In general, older males were dominant over younger ones.

Measuring associations

While some studies of wild mountain gorillas have also (or exclusively) used a proximity of <5 m (e.g., Yamgiwa 1987; Watts 1994; Robbins 1996), we elected to use a closer proximity (<2 m) for two reasons. First, we were evaluating only pair types that are known to be strong social partners and are therefore likely to spend time in close proximity to one another; second, the more conservative measure should yield the most definition in the social networks we measured. To quantify association between pairs, we used information about the time that social partners spent in close proximity (<2 m) to estimate the simple ratio index (SRI) (Cairns and Schwager 1987). To determine association index (AI) values for each pair, we calculated the proportion of point samples collected on each member of a pair:

$$\mathrm{AI} = (X^Y + Y^X)/(X + Y),$$

where X^Y is the number of times that animal Y appeared in point samples of animal X and Y^X is the number of times that animal X appeared in point samples of animal Y, divided by the sum of the visible point samples for each animal.

Social attributes

First, we used the AI matrix to construct the corresponding symmetric weighted social network. In each network, nodes corresponded to male, female, and infant individuals and the links were defined by AI values. For each individual, we calculated their eigenvector centrality, a network metric that quantifies the importance of an individual with respect to its networks (Ranhau 2000), and corresponds to the values of the first eigenvector of the graph adjacency matrix. Finally, we calculated the eigenvector centralization score for each of the social groups (group-level eigenvector), measured as the sum of the differences between the maximum vertex-level eigenvector centrality measure in the graph and the observed node-level eigenvector centrality measures. This measure was normalized in order to facilitate comparison across groups of different sizes. All network analyses were run in SNA package v.2.3-2 (Butts 2014) in R software v. 3.1.1 (R Core Team 2014).

Data analysis

To evaluate whether F–O ties were strongest, M–F ties intermediate, and M–I ties weakest in all group types (prediction 1), we first conducted a Mantel test (10,000 permutations) to compare mean AI values between the pair types and test the null hypothesis that the AIs between and within pair-type categories have the same mean (Whitehead 2008). Then, to identify specifically how AI values differed between pair types, we ran a multilevel mixed effects regression model using the AI as the response variable. We included the number of adult males, pair type (0 = M–F, 1 = F–O, 2 = M–I), a number of males–pair type interaction term, and group size as fixed effects, and both individuals' identifications plus group identification as random effects parameters. Based on the result obtained, we then ran pairwise comparisons of the predictive margins by pair type.

To test if each pair type's association strength was predicted by the number of males in a group (prediction 2), we ran mixed effects models (one for each of the three pair types) that contained number of males, group size, and infant age (for models evaluating M–I and F–O pairs only) as fixed effects and individual and group identifications as random effects parameters. In some cases the models failed to converge with all three random effects parameters included; these are reported individually in the results.

To assess if the number of females and infants was a better predictor of association strength in M–F and M–I pairs than number of males, or the ratios of males to females and males to infants (prediction 3), we first calculated the relevant ratios by taking the quotient of the male(s) divided by the number of females (or infants) in the group (from Table 1). Since females and offspring are only included in the data when both parties were present, the male:female and male:infant ratios are identical, so we use the notation F(I) when referring to this ratio in order to simplify terminology. We then fitted 3 linear mixed models [one containing number of females (or infants), the second containing number of males, the third containing the ratio of all males to F(I)] first for M–F pairs and then for M–I pairs. All models controlled for group size, and models evaluating M–I pairs also controlled for infant age. Some models failed to estimate standard errors for all 3 random effects parameters (group identification and each individual's identification). Where this occurred, we removed either group or individual identifications and report the results of the model with the lower (i.e., better-fitting) Akaike information criterion corrected for small samples (AICc) of the two (Anderson and Burnham 2002). The included random effects for each model are reported in Table 4a and b.

We identified the model that was the best fit to the data for each of the two tested pair types (M–F and M–I) using AICc. Models with difference scores of 0–2 are considered to have similar support; higher numbers indicate decreasing support compared to the best-fitting candidate model (i.e., the model with the lowest AICc value) (Anderson and

Burnham 2001; McElreath et al. 2008). We also compared the candidate models to a null model; in all cases, the null model had an AICc difference score (ΔAICc) of at least 20, indicating our candidate models were substantially better fits to the data than the null.

To test if group-level eigenvector centrality was higher in groups with fewer males (prediction 4), we used the group level measure as the response variable in a model that contained number of males as a fixed effect. Since there were a small number of groups ($n = 10$), instead of using group size in the same model, we ran the model again with group size as a continuous predictor, and compared the relative fits of the two models using the ΔAICc. Based on visual inspection of the data, we also evaluated the fit of the quadratic term for each predictor.

To evaluate if the dominant males' eigenvector centrality was lower in groups with more males (prediction 5), we fitted a linear regression model with dominant males' eigenvector values as the outcome variable. In the first model, we used number of males as a fixed effect, and as for the previously described analysis, fitted a second model containing group size for comparison via ΔAICc. Since the observations in these models are independent (i.e., group and individual identifications do not repeat), these models contained no random effects variables.

Results

First, we generated network graphs for each of the 10 groups. Visual inspection indicated close social networks with ties between most nodes (Fig. 1a, b). Neither group size nor the number of males in a group predicted AI values across pair types (group size: $B = -0.013$, SE $= 0.012$, $z = -1.09$, $p = 0.274$; number of males: $B = 0.035$, SE $= 0.030$, $z = 1.18$, $p = 0.239$).

Prediction 1

Mantel statistics indicated that AI values were distributed amongst pair types differently than chance for 8 of the 10 groups. Single-male group ISA failed to reach the $p < 0.05$ level of significance (Mantel statistic r: 0.339, $p = 0.060$). In single-male group BWE, AI values were distributed across pair types no differently than chance (Mantel statistic r: 0.172, $p = 0.177$).

Following our prediction, F–O pairs associated more than the other two pair types in all group types (Table 2; for F–O pairs $\bar{x} \pm \mathrm{SE} = 59.5 \pm 3.8$ %; for M–F pairs $= 6.2 \pm 0.6$ %; for M–I pairs $= 9.5 \pm 0.9$ %). However, contrary to our prediction, M–I associations were significantly stronger than M–F associations overall (Table 3).

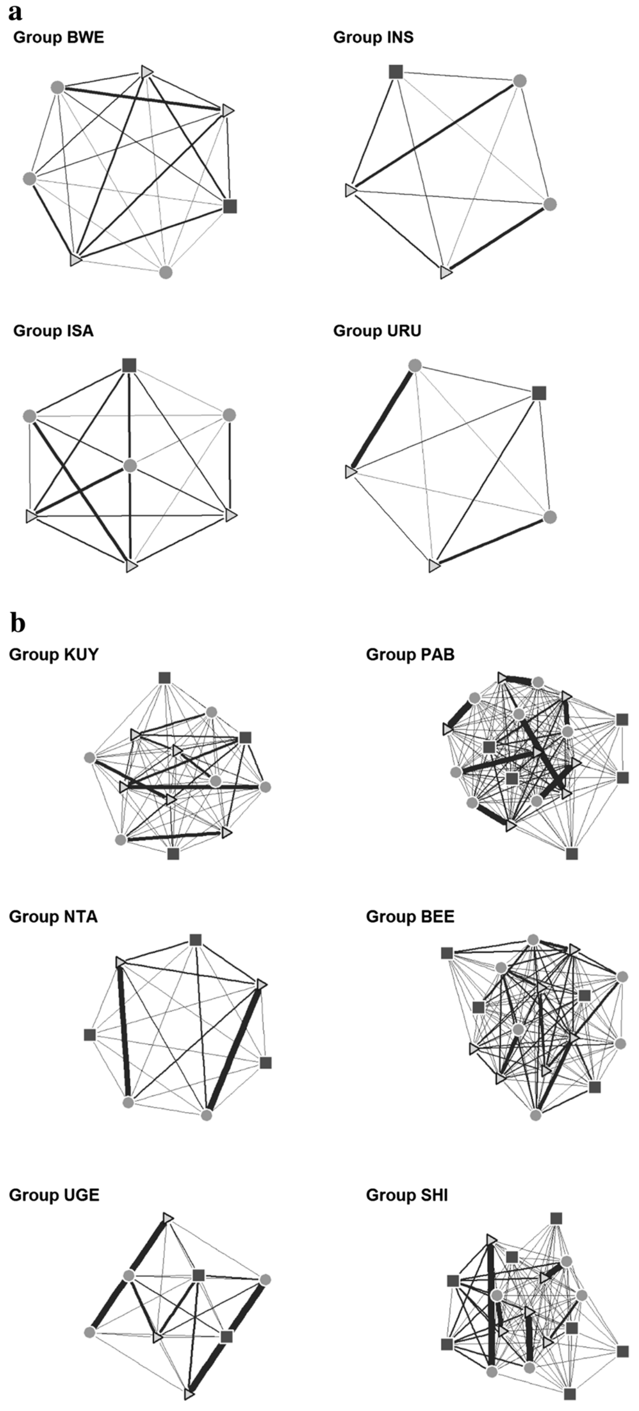

Fig. 1 **a** Social network graphs for single-male groups. *Thickness of line* represents strength of the association index value. **b** Social network graphs for groups containing 2 or 3 males (*left column*) and groups with 4+ males (*right column*). *Filled squares* adult males; *filled circles* adult females; *filled triangles* infants

Prediction 2

After controlling for group size, M–F associations were weaker in groups with more males than those with fewer males ($\beta = -0.012$, SE $= 0.006$, $z = -2.07$, $p = 0.039$,

Table 2 Relationship between pair type, number of males, the pair type–number of males interaction term, and pairs' association index value (calculated from proximity data)

Association index value	Coefficient	SE	z	p	95 % CI (lower)	95 % CI (upper)
Pair type[a]						
F–O	0.333	0.078	4.26	**0.000**	0.180	0.486
M–I	0.113	0.019	6.07	**0.000**	0.077	0.150
# of males	0.013	0.030	0.45	0.653	−0.045	0.072
Pair type[a]—# of males interaction term						
F–O	0.055	0.018	3.06	**0.002**	0.020	0.091
M–I	−0.018	0.004	−4.65	**0.000**	−0.026	−0.010
Group size	−0.015	0.011	−1.34	0.180	−0.037	0.007
Constant	0.213	0.086	2.47	0.014	0.044	0.382

Values in bold indicate a statistically significant ($p < 0.05$) relationship between the predictor variable and the index value

F–O female–offspring pairs, *M–I* male–infant pairs

[a] Reference category is male-female pairs

Table 3 Pairwise comparison of predictive margins by pair type

Association index value	Contrast	SE	z	p	95 % CI (lower)	95 % CI (upper)
M–F vs F–O	0.572	0.038	15.18	**0.000**	0.498	0.646
M–F vs M–I	0.035	0.007	5.05	**0.000**	0.022	0.049
M–I vs F–O	−0.536	0.038	14.24	**0.000**	−0.610	−0.463

Values in bold indicate a statistically significant ($p < 0.05$) difference between the listed pair types' association index values, calculated from proximity data

M–F male–female pairs, *M–I* male–infant pairs, *F–O* female–offspring pairs

$n = 123$). When only M–F pairs that contained dominant males were included, associations were the same regardless of the total number of males ($\beta = -0.014$, $\mathrm{SE} = 0.009$, $z = -1.62$, $p = 0.106$, $n = 38$; Fig. 2a). However, the very similar slopes for the M–F pairs that contained all males and those that contained dominant males suggest that the lack of effect for M–F pairs containing dominant males was a result of the small sample size (Fig. 2a). Both models that evaluated only M–F pairs failed to converge with all 3 random effects parameters specified (group identification and both partners' individual identifications), but results were the same when we removed either group or individual identifications.

After controlling for infant age and group size, M–I associations were weaker in groups with more males than in groups with fewer males ($\beta = -0.028$, $\mathrm{SE} = 0.011$, $z = -2.43$, $\mathrm{p} = 0.015$, $n = 123$). In contrast to M–F pairs and our prediction, M–I associations were also weaker in groups with more males than in those with fewer males when only pairs containing dominant males were tested ($\beta = -0.030$, $\mathrm{SE} = 0.013$, $z = -2.37$, $p = 0.018$, $n = 38$; Fig. 2b). The model containing only pairs with dominant males failed to converge with all 3 random effects parameters included, but results were the same regardless of which were removed.

Also contrary to our predictions, there was a statistical trend for F–O associations to be stronger when there were more males in the group than when there were fewer ($\beta = 0.074$, $\mathrm{SE} = 0.044$, $z = 1.69$, $p = 0.091$, $n = 38$), after controlling for infant age and group size.

Prediction 3

For M–F pairs, the model containing the ratio of all males to F(I) fit the data best, with less support for the models containing the absolute number of males or females (Table 4a). Results were similar for M–I pairs; the models containing the ratio of all males to F(I) was the best fit, with less support for the models containing either the absolute number of males or infants (Table 4b). In both cases, the fewer the number of males compared to females and infants, the more both pair types associated (for M–F pairs, $\bar{x} = -0.038$, $\mathrm{SE} = 0.014$; for M–I pairs, $\bar{x} = -0.097$, $\mathrm{SE} = 0.03$; Fig. 3). Results for both pair types contradicted our predictions.

Prediction 4

Visual examination suggested a nonlinear relationship between the number of males and group-level eigenvector centrality (single-male groups: $\bar{x} = 0.14$, $\mathrm{SD} = 0.06$, $n = 4$; multimale groups: $\bar{x} = 0.19$, $\mathrm{SD} = 0.06$, $n = 6$; Fig. 4). Group size and number of males per group were

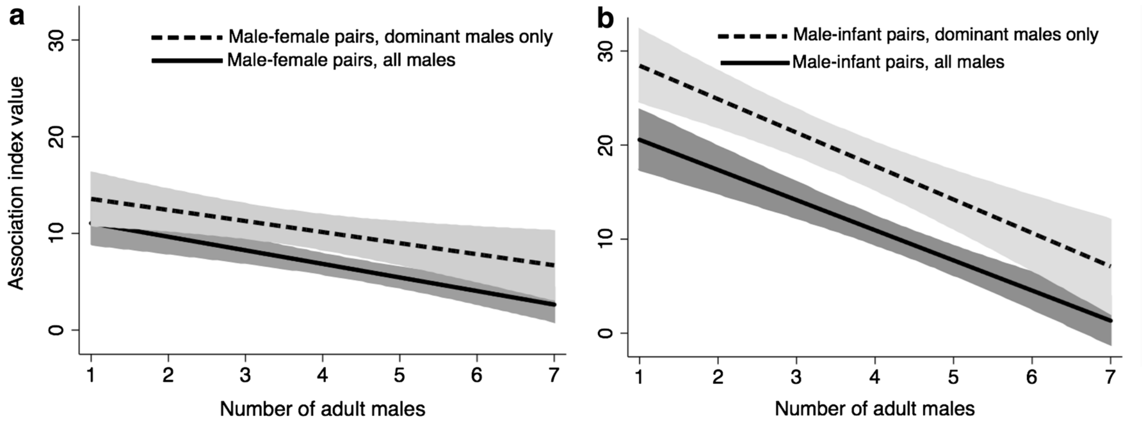

Fig. 2 **a** If all male–female pairs are included, male–female associations are weaker in groups that have more males than in those that have fewer ($p = 0.039$, $n = 123$). However, associations between dominant male–female pairs are the same regardless of the number of males in the group ($p = 0.106$, $n = 38$). **b** For both all male–infant pairs ($p = 0.015$, $n = 123$) and dominant male–infant pairs ($p = 0.018$, $n = 38$), association strength gets weaker as the number of males in a group increases

Table 4 (a) Relative model fits for male–female pairs ($n = 123$); (b) relative model fits for male–infant pairs ($n = 123$)

Model	*K*	LL	AICc	ΔAICc
(a)*				
All males:F(I)[a]	6	183.06	−353.41	0
Number of males[b]	7	182.51	−350.05	3.36
Number of females/infants[a]	6	181.31	−349.90	3.51
Null model	2	166.30	−328.51	24.90
(b)**				
All males:F(I)[b]	8	156.41	−295.55	0
Number of males[b]	8	154.96	−292.66	2.89
Number of females/infants[a]	7	152.58	−290.19	5.36
Null model	2	107.46	−201.72	93.83

K number of estimated parameters; *LL* log likelihood; *AICc* Akaike's information criterion corrected for small samples; *ΔAICc* AIC difference values

* All models include group size as a fixed effect

** All models include group size and infant age as fixed effects

[a] Individuals' identifications were included as random effects

[b] Group and both individuals' identifications were included as random effects

both unrelated to group-level eigenvector centrality (number of males: $\beta < 0.000$, SE $= 0.010$, $t = 0.01$, $p = 0.992$, $n = 10$; group size: $\beta = -0.003$, SE $= 0.004$, $t = -0.67$, $p = 0.523$, $n = 10$).

Data suggested that groups containing 2 or 3 males had higher eigenvector centrality measures than groups that contained either 1 or 4+ males (Fig. 4), so we also tested the quadratic term for both number of males and group size. In both cases, these predictor variables were unrelated to group-level eigenvector centrality (number of males: $\beta = -0.004$, SE $= 0.006$, $t = -0.63$, $p = 0.551$, $n = 10$; group size: $\beta = -0.001$, SE $= 0.001$, $t = -1.00$, $p = 0.350$, $n = 10$).

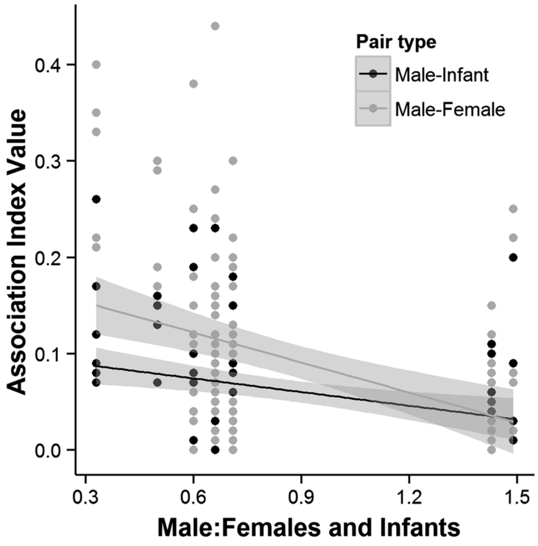

Fig. 3 The fewer the number of males compared to females and infants, the more both male–female and male–infant pairs associated. This ratio better predicted male–female and male–infant association strength than the absolute number of males, females, or infants

Prediction 5

As the number of males in a group rose, the dominant male's eigenvector centrality score decreased ($\beta = -0.019$, SE $= 0.003$, $t = -7.44$, $p < 0.001$, $n = 10$; Fig. 4). The same was true of group size; dominant males in larger groups had lower eigenvector centrality scores than dominant males in smaller groups ($\beta = -0.007$, SE $= 0.001$, $t = -6.13$, $p < 0.001$, $n = 10$).

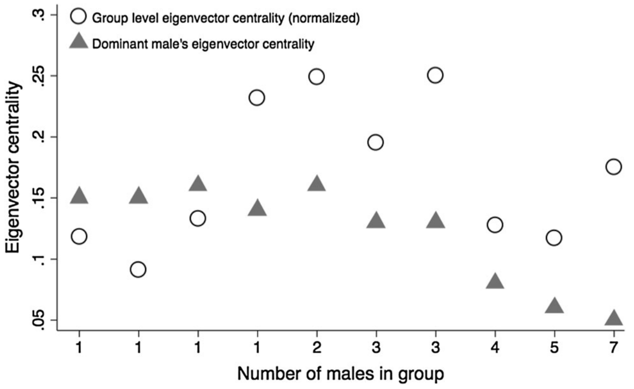

Fig. 4 Group-level eigenvector centrality (a measure of an animal's importance to its social network) was unrelated to the number of males in a group. However, dominant males in groups with fewer males had higher eigenvector centrality than dominant males in groups with more males

Discussion

Our results revealed some surprising relationships between group type, pair association strength, and the importance of dominant males to group structure in mountain gorilla groups. As expected, F–O pairs had the strongest bonds regardless of group type. However, M–I bonds were stronger than M–F, which are generally considered the primary bond in gorilla societies (e.g., Harcourt and Stewart 2007). Infants' bond strength with the dominant male, their most preferred male social partner and most likely father (e.g., Bradley et al. 2005; Rosenbaum et al. 2015; Vigilant et al. 2015), was dependent on group structure. Dominant males and infants in groups with more males (and therefore lower paternity certainty) had weaker bonds than their counterparts in groups with fewer males. Furthermore, the ratios of all males to females and males to infants were better predictors of bond strength for both M–F and M–I pairs than the absolute number of males, or the number of females and infants (i.e., the ratio of dominant male to females or dominant male to infants), despite the well-established preference of most females and infants for the dominant male (e.g., Sicotte 1994; Stewart 2001; Rosenbaum et al., in review). Dominant males also had lower measures of network centrality in groups with more males than in those with less. Together, these results suggest that (1) nondominant males play an important role in shaping social dynamics in gorilla groups despite their often peripheral positions, and (2) bonds between males and infants should be considered a key component of group structure.

The role of nondominant males

As reported in many previous studies (e.g., Harcourt 1979b; Yamagiwa 1983; Robbins and Robbins 2004), nondominant males are typically much more peripheral in mountain gorilla groups than dominant males. The dominant male is usually at the center of resting groups, guides the direction of travel, and is the most preferred social partner of the majority of females and infants. This can leave the impression that in multimale groups, the dominant male plus females and offspring essentially comprise a harem system inside a loose multimale/multifemale structure. While the dominant male is undoubtedly the most important adult male social partner for most females and infants, these analyses make it clear that the presence of additional males not only affects reproductive opportunities (e.g., Robbins et al. 2014; Vigilant et al. 2015) but also influences the social ties between the dominant male and females and infants. If nondominant males were irrelevant, then the number of females and infants should have been a better (or at least equally good) predictor of association strength than the ratio of all males to females and infants, but it was not. Also, having additional males in the group meant that the dominant male was less important to group structure (i.e., had lower eigenvector centrality) than the dominant male in groups with fewer males.

The influence of nondominant males on social relationships has potential implications for female life histories. Some evidence suggests females are less likely to transfer out of multimale groups (Robbins et al. 2009; 2013), where there tend to be more males per female. Females with more competition for social access to males had the strongest relationships with them. This suggests they may be working harder to maintain these relationships than females with less intrasexual competition; previous work indicates that females are generally more responsible for maintaining proximity to males than males are to them (e.g., Watts 1992), though proximity maintenance data are needed to test whether this is true regardless of the number of available males. More frequent transfers by females in single-male groups (Robbins et al. 2009, 2013) may be partially motivated by elevated intrasexual competition. Living in multimale groups and cultivating multiple weaker social bonds with males may be an advantageous reproductive strategy since protection is then virtually assured even if one male disperses or dies (Robbins et al. 2013). Females apparently value the presence of these additional males, but instead of fostering close social relationships with them, they demonstrate it via higher social group fidelity.

The role of male–infant relationships

Gorilla groups have long been known to be based on M–F bonds. While we do not refute the importance of these relationships (M–I relationships would not exist without M–F associations), it is important to acknowledge the significant role that relationships between males and infants play in group structure. When compared to species (e.g., *Callitrichidae*) where males invest heavily in their offspring, male gorillas do extremely little overt parenting, but their close bonds (demonstrated in both the current study and in e.g., Yamagiwa 1983; Stewart 2001; Warren and Williamson 2001) are best explained as paternal care (Rosenbaum et al. 2011). M–I pairs associated more than M–F pairs, despite M–F bonds repeatedly being described as the strongest relationships in mountain gorilla groups (e.g., Harcourt and Stewart 2007). However, socioecological theory would predict M–I relationship strength to vary systematically with group type, as a proxy for paternity certainty. These data support the predictions of the models: bonds were weakest in groups where paternity certainty was lowest. While the dominant male is the most likely father of a given infant in a multimale group, nondominant males also sire infants, and this population has shown considerable variation in reproductive skew (Bradley et al. 2005; Rosenbaum et al. 2015; Vigilant et al. 2015). More data are needed to determine if changes in bond strength track reproductive skew fluctuations.

The strength of M–I bonds could have implications for group structure and fitness consequences well past infant vulnerability to infanticide and predation. In this species, mature males can remain in their natal group or disperse, but staying has better fitness outcomes for subordinates (Robbins and Robbins 2004). This is likely the ultimate cause of multimale groups. In such groups, infants' proximity relationships with adult male social partners predict their proximity relationships with the same males when they mature into subadults and then young adults (Rosenbaum et al., in review). Since these early relationships apparently last across multiple developmental stages (juvenile to subadult to young adult, or at least 7 years; Rosenbaum et al., in review), we speculate that these relationships might be a proximate mechanism contributing to the persistence of multimale groups in mountain gorillas. Stoinski and colleagues (2009b) found that males with co-resident mothers were less likely to disperse than other males even though such relationships no longer had any obvious benefits. More work is needed to determine whether subordinate male dispersal decisions might also be associated with their early-life bonds with adult males (e.g., Harcourt and Stewart 1981). The fluctuating group structure of mountain gorillas makes them a particularly interesting species in which to examine the downstream effects of early relationships.

Conclusions

Nuances of dyadic social relationships are affected by myriad factors, including other social partners and the activity in which social partners are engaged. When considering the relative strength of relationship types, it is important to bear in mind that factors such as physical constraints on space near social partners and/or perceived feeding competition may affect proximity measures. Additional analyses that address specific effects of group and individual activity, as well as additional outcome variables such as other proximity categories or alternative affiliative behaviors, will help illuminate the role such factors play in determining stochastic variation in relationship strength. The individual relationships underlying mountain gorillas' fluctuating social structure are a particularly rich topic of investigation for those interested in the evolution of *Homo sapiens*' highly variable social structure.

The analyses presented here add to our understanding of the complexity of variability in gorilla social structure. Individuals living in varying social configurations can be characterized by important differences in social relationship strength between males and females, and between males and infants, which may have life history and fitness consequences. Attention must be paid to these underlying differences when interpreting behavior across social structures. We hope that similar comparisons of bond strength by pair type will soon be available for western gorillas, chimpanzees, and bonobos, whose varying socioecologies would make them interesting points of comparison for these findings.

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Compliance with ethical standards

Conflict of interest and statement on the welfare of animals The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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