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Male rank, not paternity, predicts male–immature relationships in mountain gorillas, *Gorilla beringei beringei*

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Kin discrimination mechanisms are expected to evolve when they provide fitness benefits. To date, evidence for kin discrimination is mixed across taxa and mating systems even when it would apparently be beneficial. In animals with promiscuous mating systems, males were long believed to abstain from parenting behaviours partly because the costs of offspring misidentification outweighed the benefits of dual parenting. Conversely, males in monogamous systems could parent because of high paternity certainty. However, recent work has shown that in some species males parent despite high false paternity rates, and males in some promiscuous systems discriminate between their own and other males' offspring. Here we evaluate the impact of male dominance rank, paternity and age on male–immature relationships in wild mountain gorillas. Mountain gorillas provide an interesting context for assessing paternal kin discrimination because (1) male–immature relationships are strong, and (2) while their morphological characteristics suggest an evolutionary history of single-male groups, a substantial fraction contain multiple adult males. In our sample of 21 males and 49 genotyped immatures living in multimale groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center, we found that male rank was the primary predictor of male–immature relationship strength. There was little evidence that paternity or age were related to relationship patterns. Male–immature dyads were closer social partners in 2011–12 when groups were smaller and reproductive skew lower, than comparable dyads in 2003–04 when groups were larger and skew higher. Gorillas' lack of paternal kin discrimination provides further behavioural evidence that the species' multimale social structure is evolutionarily novel. However, patterning of male–immature relationships and genetic paternity suggest a persistent minority of two-male groups throughout *G. beringei's* evolutionary history. This may help explain their ability to live in multimale, multifemale social units despite possessing morphological characteristics typical of harem systems.

Kin discrimination is useful when social structure facilitates cooperative behaviour (Hamilton, 1964) or enables deleterious inbreeding (Blouin & Blouin, 1988; Lehmann & Perrin, 2003). Accordingly, selection pressure should favour kin discrimination in systems in which costs of misidentification are high, or when the benefits of cooperation are particularly valuable. Examples include socially monogamous species in which one partner may be cuckolded (e.g. New World primates: Achenbach & Snowdon, 2002; Mendoza & Mason, 1986; Tardif, Carson, & Gangaware, 1990; rodents: Cantoni & Brown, 1997; Jones & Wynne-Edwards, 2000; Silva, Vieira, & Izar, 2008; Wynne-Edwards, 1987; birds: Wan, Chang, & Yin, 2013; Webster, Tarvin, Tuttle, & Pruett-Jones, 2007; reviewed in Cockburn, 2006; fish: Balshine-Earn & Earn, 1997; DeWoody, Fletcher, Wilkins, & Avise, 2000; Itzkwitz et al., 2001) or species that rely heavily on cooperative behaviour for mating access, offspring rearing, territory control or food acquisition (e.g. social insects: reviewed in Beshers & Fewell, 2001; Old World primates: Mitani, Merriwether, & Zhang, 2000, Muller & Mitani, 2005, reviewed in Silk, 2002; social carnivores: de Villiers, Richardson, & van Jaarsveld, 2003; Mosser &

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Packer, 2009; Packer & Pusey, 1982; communal rearers such as eiders (Öst, Smith, & Kilpi, 2008; Öst, Ydenberg, Kilpi, & Lindström, 2003) or house mice (König, 1994; Weidt, Hofmann, & König, 2008)). Selection pressure for kin discrimination should also be strong in the relatively few species in which juveniles routinely reach sexual maturity while living with close kin of the opposite sex (e.g. capuchins, *Cebus capucinus*: Muniz et al., 2006; northern muruquis, *Brachyteles hypoxanthus*: Strier, Chaves, Mendes, Fagundes, & Di Fiore, 2011; mountain gorillas: Robbins, Stoinski, Fawcett, & Robbins, 2009; Stoinski, Vecellio, et al., 2009).

To date there is mixed evidence for kin discrimination across taxa and mating systems. Most bird species are socially monogamous and provide biparental care. However, although ~11% of offspring are a result of extrapair paternity (Griffith, Owens, & Thuman, 2002), males generally do not discriminate on the basis of paternity (Kempnaers & Sheldon, 1996). Pair-bonded fat-tailed dwarf lemurs, *Cheirogaleus medius*, have high rates of extrapair paternity (44%), but males do not reduce care to unrelated infants (Fietz et al., 2000). There is scant evidence for kin discrimination in social insects with multiple-queen colonies or low overall relatedness (e.g. social wasps: Strassmann et al., 1997; Strassmann, Seppä, & Queller, 2000; honeybees: Châline, Martin, & Ratnieks, 2005; ants: Friend & Bourke, 2012; Holzer, Kümmerli, Keller, & Chapuisat, 2006).

However, despite the apparently poor cuckold detection abilities of male birds and fat-tailed lemurs, and the indiscriminate cooperation of many social insects, many animals clearly do recognize and interact preferentially with kin. This includes some insects (e.g. Lihoreau & Rivault, 2009; Lizé, Carval, Cortesero, Fournet, & Poinsot, 2006) social carnivores (e.g. Leclaire, Nielsen, Thavarajah, Manser, & Clutton-Brock, 2013; Wahaj et al., 2004) and many primates (e.g. Albers & Widdig, 2013; Charpentier, Peignot, Hossaert-McKey, & Wickings, 2007; Eberle & Kappeler, 2006; Huchard et al., 2012; Langos, Kulik, Mundry, & Widdig, 2013; Wikberg, Ting, & Sicotte, 2014; reviewed in Silk, 2002, 2006). In the few primate species in which single-sex dispersal does not preclude inbreeding, discrimination mechanisms appear to minimize the likelihood that it occurs (e.g. Muniz et al., 2006; Packer, 1979; reviewed in Pusey, 1990).

In mammals, maternal kin discrimination is simple. Gestation, birth and lactation are reliable cues for maternal kin detection. For fathers, the task is more difficult. In species that form pair bonds or single-male groups, males may use proxies such as coresidence to detect offspring, but the reliability of these proxies varies across species. For example, the high rates of extrapair copulations in socially monogamous birds and lemurs cited above suggest that selection pressure is generally not strong enough to encourage more sophisticated discrimination systems. Mammalian fathers in multimale groups cannot rely on residence cues, particularly in species in which females regularly mate with more than one male during periods of sexual receptivity. For years it was assumed that paternity uncertainty limited males' investment in offspring in such species. However, advances in noninvasive molecular genetics have enabled rigorous testing of this hypothesis in wild populations, and the results have been surprising. In primates, there is evidence for father–offspring discrimination in nonmonogamous chimpanzees, *Pan troglodytes* (Lehmann, Fickenscher, & Boesch, 2006), baboons, *Papio cynoceophalus* (Buchan, Alberts, Silk, & Altmann, 2003; Charpentier, Van Horn, Altmann, & Alberts, 2008; Huchard et al., 2012), mandrills, *Mandrillus sphinx* (Charpentier et al., 2007), capuchins (Muniz et al., 2006), rhesus macaques, *Macaca mulatta* (Langos et al., 2013) and langurs, *Presbytis entellus* (Borries, Launhardt, Epplen, Epplen, & Winkler, 1999). The domains in which paternal kin discrimination appears include affiliative behaviour, mate choice and protection against infanticide.

Mountain gorillas are unusual among primates because they regularly form both single-male and multimale groups. About 40% of the gorilla groups in central Africa's Virunga massif are multimale (Gray et al., 2010). Large numbers of adult males (range 2–9) have co-resided for years in mixed-sex groups, with remarkably high male-to-female ratios (Stoinski, Rosenbaum, et al., 2009). It is unclear whether there would have been evolutionary pressure for paternal kin discrimination to develop in mountain gorillas. This is likely to depend on how common multimale groups have been in the species' evolutionary history, and how important paternal care is to offspring. Gorillas have the physical characteristics of a species that primarily relies on contest competition, including marked sexual dimorphism in body size, well-developed weaponry, small testicles relative to body size and slow-swimming sperm (Crook, 1972; Harcourt, Harvey, Larson, & Short, 1981; Leutenegger & Kelly, 1977; Møller, 1988). Extragroup mating has never been reported, and there are few known instances of females successfully raising offspring in groups where they were not conceived (long-term records from the Dian Fossey Gorilla Fund's Karisoke Research Center). Thus, if single-male groups were historically the norm and there were few extragroup matings, co-residence would be a reliable proxy for paternity and preclude selection for a more sophisticated recognition mechanism.

Mountain gorillas are not only capable of living in multimale groups, they may actually benefit from doing so. Advantages to living in multimale groups include better female retention, since females seem to prefer multimale groups, and lower risk of infanticide (Robbins et al., 2013). Infanticide is two to three times more common in single-male groups than in multimale groups (Robbins et al., 2013), primarily because infants in single-male groups are unprotected if the male dies. Infants in multimale groups are still generally safe even if the dominant male dies, since other males in the group can deter infanticidal outsiders. Furthermore, queuing behind a dominant male is an effective reproductive strategy for subordinate males (Robbins & Robbins, 2005). These benefits to both males and infants suggest such groups may have regularly occurred during the species' evolutionary history; if so, then there may well have been selection pressure for paternal kin discrimination.

In mountain gorillas, both sexes have the option to disperse (for females, joining an established group or lone male; for males, starting a new group after a solitary period) or reproduce in their natal group (Harcourt, Stewart, & Fossey, 1976; Robbins, 1999; Robbins et al., 2009; Watts, 1991, 2000). Since females can reside with their fathers past the age of sexual maturity, females, and to a lesser extent fathers, would benefit from kin discrimination to avoid inbreeding (Robbins et al., 2009). Fathers and sons can also both benefit from discrimination if fathers selectively tolerate sons of breeding age who would otherwise be solitary. Sons gain reproductive opportunities, and fathers gain inclusive fitness benefits plus enhanced group defence. Previous studies hint that paternal kin discrimination may exist. Data from both Karisoke and Bwindi National Park, Uganda, suggest patrilineal relatedness may be important during life history decisions such as group fissions (Nsubuga, Robbins, Boesch, & Vigilant, 2008) and dispersal (Harcourt & Stewart, 1981). Furthermore, young gorillas have more stable social preferences for males who are old enough to have sired them, even if the male was not then dominant (Rosenbaum et al., n.d.).

Adult male and infant/juvenile mountain gorillas are close social partners (Stewart, 2001; Yamagiwa, 1983). Behavioural data analyses suggest that such relationships are best explained as a form of low-cost paternal behaviour, although they may sometimes also

function as a form of mating effort (Rosenbaum, Silk, & Stoinski, 2011), but the strength of this conclusion is limited by lack of genetic paternity data. Although the dominant male is the most likely father of any given immature (in the 1990s, 85% were sired by an alpha male; Bradley et al., 2005), reproductive skew appears to have declined since that time. During the 2000s the number of males per group increased and male-to-female ratio decreased, which corresponded with an increase in mating activity by nondominant males during windows of probable conception (Stoinski, Rosenbaum, et al., 2009) and lower reproductive skew (Vigilant et al., 2015). About 25% of young animals spend more time with a nondominant male than they do with the dominant male (Rosenbaum et al., 2011), indicating that there is variation in young gorillas' social preferences. Here we evaluate whether male dominance rank, paternity, male age at infant birth or some combination of these variables best predict the pattern of male–immature interactions in multimale mountain gorilla groups.

METHODS

Subjects and Data Collection

This study was conducted on the habituated mountain gorilla population monitored by the Karisoke Research Center (KRC) in Volcanoes National Park, Rwanda. Data were collected by the first author in 2003–2004 (508 h), and the first and second authors in 2011–2012 (1019 h), using 50 min focal follows of adult males (both time periods) and immatures (2011/2012 only). The observers conducted regular interobserver reliability tests in 2011–2012. Additional data were derived from the long-term KRC database. Analyses of proximity patterns were based on instantaneous point samples, which were available from the focal observations and the long-term records. Faecal samples for noninvasive paternity analysis were collected by the observers and other KRC staff, who were tested on individual identification of the animals. The total data set included 49 individual immatures and 21 individual adult males. The mean number of hours of focal data per dyad in 2003–2004 was 25.9 (minimum = 11.8, maximum = 38.4), and the mean number of point samples was 229 (minimum = 99, maximum = 771). In 2011–2012, the mean number of hours of focal data per dyad was 57.8 (minimum = 14.5, maximum = 99.8), and the mean number of point samples was 426 (minimum = 100, maximum = 795).

Dyad Structure

The dyad was the unit of analysis. Each dyad was made up of an adult male (≥12 years old) and an immature (1–5.9 years old, Watts & Pusey, 1993; mean ± SD = 3.4 ± 1.56 years). To be included in these analyses, the adult male partner must have been at least 8 years older than the immature partner (mean = 16.9 years, minimum = 8.1, maximum = 32.5). Although fully adult males sire most infants, one male in this population sired an infant when he was only 8 years old. This male/infant dyad is included in our analyses, even though the male was less than 12 years old when data were collected. This is the only dyad that falls outside the defined age criteria.

Adult male rank was determined using displacement patterns, as described in Stoinski, Rosenbaum, et al. (2009). Adult males are categorized as alpha (rank 1), beta (2), gamma (3) or subordinate (4). There are rarely enough displacements to determine exact ranks beyond rank 3, so all other adult males are classified as subordinates and assigned rank 4. In general, older males are dominant over younger ones.

Group Structure

Group size and mean number of males and immatures per group were all larger in 2003–2004 than in 2011–2012 (Table 1; values are as of the midpoint of each data collection period). In 2003–2004 we included every animal available in KRC's three multimale research groups; in 2011–2012, we included three of five multimale groups. The other two were excluded because at the time of data collection the number of available immatures was less than or equal to two.

Behavioural Measures

We evaluated 13 behavioural variables (Table 2). Definitions follow standards used in numerous studies on this population, with the exception of co-feeding. To our knowledge, co-feeding has not been measured in gorillas before. It was included because the first author noted that adult males appear much more tolerant of immatures feeding in close proximity to them than they are of older social partners.

Positively correlated behaviours were used to create composite indices for each dyad (see Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013). For each of the behavioural components included in a given index, we divided the value for a particular dyad by the mean value for all dyads. We then summed the quotients and divided by the number of components to obtain a composite value. High values of the composite index represent dyads that engaged in those behaviours more than the average dyad, and low values represent dyads that engaged in them less than the average dyad. We created one index based on rates of resting in physical contact and grooming (for linear mixed model regressing resting in physical contact on grooming: $\beta \pm SE = 3.21 \pm 0.32$, $Z = 9.90$, $N = 203$ dyads, $P < 0.000$), and a second index based on rates of touching and social staring ($\beta \pm SE = 0.65 \pm 0.21$, $Z = 3.11$, $N = 203$ dyads, $P = 0.002$).

Genetic Paternity

We collected faecal samples from infants, mothers and all potential fathers for noninvasive genetic paternity analysis. Sample preservation was done using the ethanol–silica storage method described in Nsubuga et al. (2004). After DNA extraction we genotyped samples at 16 autosomal microsatellite loci using the approach outlined in Arandjelovic et al. (2009), including appropriate replication of results to avoid errors such as allelic dropout. Sex was confirmed or determined using a PCR-based sexing assay (Bradley, Chambers, & Vigilant, 2001).

Sample IDs were confirmed by comparing known mother/infant pair genotypes or by comparing the genotypes obtained from two or more samples asserted to be from the same individuals. All males 7 years of age or older resident in the group at the time of conception (Bradley et al., 2005) were considered as possible sires. The mean number of potential sires per infant was 5.8 (range 1–14). We used CERVUS 3.0.3 to assess likelihood of paternity (Kalinowski, Taper, & Marshall, 2007) and required a 95% confidence level for paternity assignment. Then, we conducted simulations that assumed either

Table 1
Mountain gorilla group composition by study period

Study period	No. of groups	Mean (range)			
		Group size	Males	Females	Immatures
2003–2004	3	36 (24–58)	6.33 (6–7)	11.33 (8–17)	9.66 (5–17)
2011–2012	3	23 (12–42)	3 (2–5)	7 (4–11)	5.66 (4–9)

Table 2
Definitions of behavioural variables

Behaviour	Definition	Directional?	Collection method*
Approach/leave interaction	One individual moves into or out of 2 m range of another individual. Must remain within 2 m for at least 5 s	Yes	CFS
Time in close/medium proximity	Within 2 m/2–5 m of another animal, outside of aggressive interactions	No	ISS
Groom	One animal manipulates another's pelage with mouth or fingers	Yes	CFS; D
Rest in contact	One animal rests any body part on any part of another's body for at least 5 s	When initiator observed	CFS; D; ISS
Play	Nonaggressive interaction with both partners participating actively, engaging in behaviours such as hit, push, hold, wrestle, chase, play face, soft grunting, etc.	No	CFS; D; AL
Social stare	One individual approaches to within 1 m of another and looks intently at them, outside the context of an aggressive encounter	Yes	CFS
Touch	Affiliative contact that involves touching another individual with a foot or hand outside of any other affiliative behaviours (e.g. play, grooming)	Yes	CFS
Co-feed (2011–2012 only)	Two individuals feed within 1 m of each other. Food source(s) of each individual must also be within 1 m of feeding partner	No	CFS; AL
Follow (2011–2012 only)	Individual gets up and walks directly in the path of an individual, leaving a resting or feeding space. Must be within 2 m and 5 s of the first animal leaving; must walk in direct path for at least 5 m	Yes	CFS
Carry	An adult male moves at least 2 m transporting an infant ventrally or dorsally	Yes	CFS; AL
Hold (2011–2012 only)	An adult male picks up and holds an immature in his arms while sitting in one location	Yes	CFS; AL
Vocal aggression	One individual grunts or screams at another	Yes	CFS; AL
Noncontact aggression	One individual directs the following behaviour(s) at another in the context of an antagonistic encounter: display, chest beat, lunge, chase, or strut stance, without making physical contact	Yes	CFS; AL
Contact aggression	One individual hits, bites, kicks, pushes or otherwise physically contacts another in the context of an antagonistic encounter	Yes	CFS; AL

* CFS: continuous focal animal sampling; ISS: 10 min instantaneous scan samples; D: duration collected; AL: ad libitum sampling.

five or nine potential sires and that 10% of potential sires were related at the half sibling level ($R = 0.25$). The simulations assuming five potential sires and nine potential sires were applied to data sets consisting of offspring with six or fewer potential sires and seven or more potential sires per offspring, respectively. Simulation results were the same when we used simulations with different numbers of potential sires or increased proportions of relatives among the potential sires. We also compared offspring, mother and potential sire genotypes for genotypic incompatibilities ('mismatches'). The paternity information used here represents a subset of a larger set of paternity assessments described in detail elsewhere (Rosenbaum, Hirwa, Silk, Vigilant, & Stoinski, 2015; Vigilant et al., 2015).

Paternity was distributed among the males differently during the first data collection period and the second. In our 2003–2004 sample of 33 immatures, 28 were sired by alpha males (85%), one by a beta male (3%), three by gamma males (9%) and one by a subordinate male (3%). This is very similar to the paternity distribution described for this population by Bradley et al. (2005). There was considerably less reproductive skew among the 2011–2012 sample of 16 immatures of known paternity. Six were sired by alpha males (38%), one by a beta male (6%), two by gamma males (13%) and seven by subordinate males (44%). In the dyadic analyses reported below, we use the rank of the male when the behavioural data were collected, not the rank of the male at the time that the immature partner was conceived. Only two males changed rank between the time of conception and the time behavioural observations were made; one rose from gamma to beta, and one dropped from alpha to gamma. The mean age difference between fathers and offspring was 22.4 years in 2003–2004 (minimum = 9.6, maximum = 28.1), and 16.0 years in 2011–2012 (minimum = 10.4, maximum = 32.5). Fathers were significantly younger in the 2011–2012 sample than in the 2003–2004 sample (Mann–Whitney U test: $Z = 3.58$, $P < 0.000$; Fig. 1).

There were five immatures living in groups without their father during the 2011–2012 data collection period. Three were sired by a subordinate male who dispersed from the group shortly after they were born. The other two infants were born to females who immigrated into the study groups during the early stages of pregnancy. Four of these five are included in the above reproductive skew percentages; the fifth was excluded because he was sired by a male of unknown rank in a group not monitored by KRC. These five

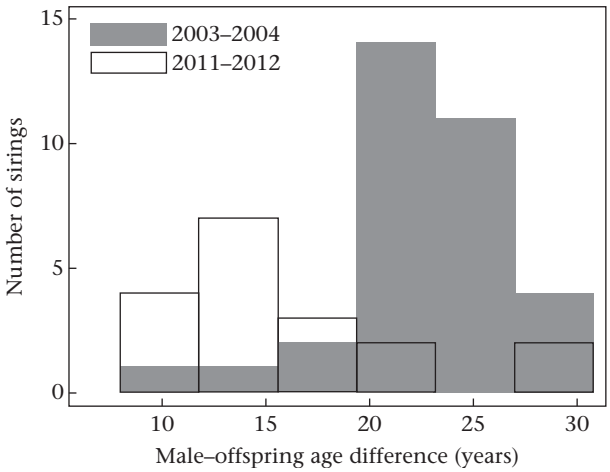

Figure 1. Age difference between mountain gorilla fathers and offspring in the 2003–2004 sample and in the 2011–2012 sample.

immatures were older than the rest of the sample (mean ± SD age of immatures with fathers present = 3.25 ± 1.54, minimum = 1, maximum = 5.9, $N = 45$; mean age of immatures without father present = 4.72 ± 1.16, minimum = 3.2, maximum = 5.9, $N = 5$; Mann–Whitney U test: $Z = 1.96$, $P = 0.050$). These immatures were only included in analyses in which they were explicitly compared to immatures who lived in their sire's group.

Data Summary

Rates of behaviours were calculated for each male–immature dyad, controlling for the amount of time visible and the amount of time the two individuals were co-resident in the group. To determine which member of the dyad was primarily responsible for maintaining proximity, we calculated Hinde index values (Hinde & Atkinson, 1970):

$$H = (\mathrm{IA}/(\mathrm{IA} + \mathrm{MA})) - (\mathrm{IL}/(\mathrm{IL} + \mathrm{ML}))$$

where MA is the number of times the adult male partner approached the immature partner, IA is the number of times the immature partner approached the adult partner, ML is the number of times the male left the immature, and IL is the number of times the immature partner left the male. This computes a proportion between −1 and 1; higher values indicate that the immature was more responsible for proximity maintenance, and lower values indicate that the adult male was. Hinde index values were computed for all dyads with at least 10 approach/leave interactions.

Data Analysis

All analyses were performed in Stata 13. We used multilevel, mixed effects regression models that treated individual animal IDs as a random effects parameter. Ad libitum data were used strictly as count data rather than calculating a rate. Visual examination of the data revealed possible differences in behavioural outcomes between the 2003–2004 sample and 2011–2012 sample. We used a dummy variable to evaluate study period effects, coded as 0 for the 2003–2004 sample and 1 for the 2011–2012 sample.

For each outcome variable, we evaluated 15 models; four with a single predictor variable (male rank, age difference, paternity or study period), then all possible combinations of two or three of those variables, and finally a model containing all four variables. We ranked the models using adjusted Akaike information criteria (AICc). The model with the lowest AICc score is the model with the most support (Anderson, Link, Johnson, & Burnham, 2001; McElreath et al., 2008). Here, we present the model with the most support, plus any additional models with an AICc difference score (ΔAICc) of ≤5. Difference scores of 0–2 indicate similar support for the relevant models; higher numbers indicate increasingly less support. Models are penalized for each additional variable, which prevents overfitting of data. In addition to the AICc and ΔAICc, we also report Akaike weights (ωAICc). The weight for a given model may be interpreted as the probability that the model is the best fit out of all candidate models tested (Anderson & Burnham, 2002; e.g. House, Henrich, Sarnecka, & Silk, 2013).

Post hoc, we tested models containing two-way interaction effects between male rank and paternity, age difference and paternity, and study period and paternity, but in most cases models containing these interactions had substantially higher AICc scores (>10) than models without. Because there was little evidence that these models were appropriate fits for the data, we dropped them from our overall model selection and report only the main effects models described above. We also experimented with a quadratic term for the age difference predictor, since the relationship between age difference and our outcome variables was not always linear; very old males, and males on the young end of the distribution often are more peripheral to the group and so interact less often with immatures. However, the quadratic term did not improve the fit of any models, and in most cases raised the AICc ≥5. Therefore, we did not include the models with the quadratic term in our set of candidate models.

To determine whether the five immatures living in social groups without their father had different relationships with adult males than those whose father was present, we used standard hypothesis testing methods. For each outcome variable, we ran the same multilevel mixed-effects models described above with a father absent/present dummy variable. Each model controlled for male rank and age of the immature. Male–immature age difference was not included in these models because the analyses were conducted after results from the primary analyses were available, so we were already aware of the relationship between our outcome variables and age difference.

RESULTS

Time in Proximity

Male–immature dyads spent more time in close proximity if the male partner was high ranking and if they were in the 2011–2012 study period. Two models had equal support: the model containing male rank and study period and the model containing male rank only (Table 3). Weights suggest that the model including both rank and study period was the most appropriate choice (Table 3). Visual inspection indicates that the study period effect was driven by dyads with alpha and beta males; these dyads spent more time together in the 2011–2012 study period, while dyads with gamma and subordinate males were very similar in both periods (Fig. 2).

As with close proximity, dyads spent more time in medium proximity (2–5 m) if they contained high-ranking males and if they were in the 2011–2012 study period. The model containing only rank was the best fit (Table 3). There was moderate support for the second-ranked model that contained both rank and study period (Table 3).

Proximity Maintenance Behaviours

Immatures worked harder to maintain proximity to higher-ranking males than to lower-ranking ones (Table 4, Fig. 3). They were also more likely to follow higher-ranking males, but we were only able to evaluate this in the 2011–2012 study period (Table 4).

Table 3
Time in proximity ($N = 176$ dyads)

	Model	LL	*K*	ΔAICc	ωAICc
Close proximity	Rank[1]+study period[2] [1]β±SE=0.050±0.008 [2]β±SE=0.043±0.013	259.55	6	0	0.63
	Rank β±SE=0.056±0.007	257.79	5	1.39	0.31
Medium proximity	Rank β±SE=0.028±0.004	333.46	5	0	0.74
	Rank[1]+study period[2] [1]β±SE=0.025±0.005 [2]β±SE=0.022±0.009	332.68	6	3.71	0.12
	Rank[1]+age difference[2] [1]β±SE=0.020±0.005 [2]β±SE=0.003±0.001	332.49	6	4.10	0.10

LL: log likelihood; *K*: number of estimated parameters; AICc: difference in adjusted AIC values; ωAICc: weight of adjusted AIC values.

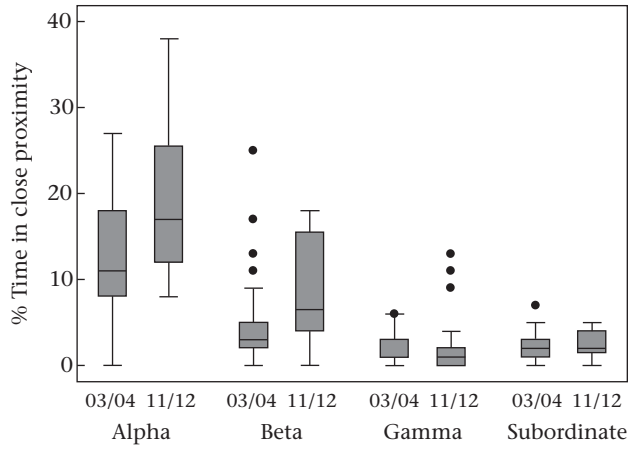

Figure 2. Percentage of time that male and immature mountain gorillas spent in close proximity based on male rank and study period (03/04: 2003–2004; 11/12: 2011–2012).

Table 4
Proximity maintenance behaviours

	Model	LL	*K*	ΔAICc	ωAICc
Hinde index values	Rank	32.20	5	0	0.90
(*N*=94 dyads)	β±SE=0.095±0.018				
Follow rates (2011–2012 only)	Rank	39.72	5	0	0.90
(*N*=44 dyads)	β±SE=0.071±0.028				

LL: log likelihood; *K*: number of estimated parameters; AICc: difference in adjusted AIC values; ωAICc: weight of adjusted AIC values.

The model containing only male rank was the best fit for both Hinde index values and following behaviour (Table 4). Second-best models in both cases had ΔAICc of >5.

Affiliative Behaviours

Resting in contact and grooming

No one model clearly best fit the composite rest in contact/grooming scores (Fig. 4). Two performed equally well: rank and study period, and rank/paternity/study period (Table 5). Once again, dyads with high-ranking males and dyads in the 2011–2012 study period spent more time resting in contact and grooming.

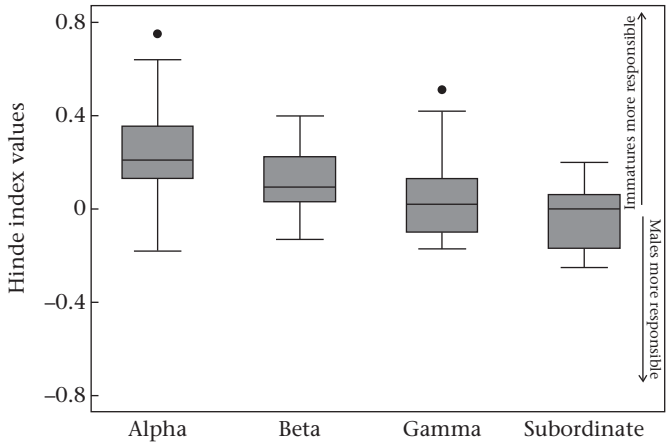

Figure 3. Hinde index values, calculated from approach/leave interactions, for male–immature dyads. Higher values indicate that immatures were more responsible for maintaining proximity; lower ones indicate that males were.

Two additional models had ΔAICc of <2: rank/age difference/study period and a model containing all four predictors. The beta coefficient for age difference was negative, indicating that dyads closer in age groomed and rested in contact more than dyads with a bigger age gap. Although the paternity variable was included in two models with ΔAICc of <2 and the beta coefficient was positive (indicating father/offspring dyads affiliated more), in both cases the standard error was larger than the coefficient (Table 5). It is therefore difficult to draw reliable conclusions about the relationship between paternity and our rest in contact/grooming measure. Both rank and study period were clearly better predictors of resting in contact and grooming than the other variables (Fig. 4).

Touching and social staring

Dyads containing high-ranking males touched and stared more often. The rank-only model performed best for the composite touch/staring measure (Table 5). Two other models had ΔAICc of <2 (rank/paternity and rank/study period), but the ωAICc indicates that a model containing only rank was the most probable. Father/offspring dyads engaged in these behaviours less than unrelated dyads. High standard errors prevent reliable conclusions about the relationship between study period and touching/social staring (Table 5).

Playing

Dyads containing lower-ranking males played more than dyads that contained high-ranking males (Table 5). Models containing any other predictor variables had ΔAICcs of >6.

Aggressive Behaviours

Rates of all types of aggression were extremely low, but 34 of 176 dyads (19%) engaged in at least one bout of vocal aggression. Eleven (6%) engaged in at least one bout of noncontact aggression, and 11 dyads (6%) engaged in at least one instance of contact aggression.

Vocal aggression

Low-ranking males vocally threatened their immature partners more often than did high-ranking males (Table 6). Models containing any other predictor variable performed much worse (ΔAICc >8) than the rank-only model.

Noncontact aggression

High-ranking males directed noncontact aggression at immature partners more often than did low-ranking males (Table 6). Again, the model containing only rank performed far better than any other model; the second-best model had a ΔAICc >9.

Contact aggression

Dyads in the 2003–2004 study period engaged in more contact aggression than dyads in the 2011–2012 study period (Table 6). The paternity-only model had a ΔAICc of <2, but the standard error was larger than the beta coefficient for both this model and the rank-only model (Table 6). The ωAICc indicates that the study period-only model was the best choice.

Feeding Tolerance

In the 2011–2012 study period, dyads containing high-ranking males co-fed more than dyads with low-ranking males (Table 7). The rank-only model performed best. All other models had a ΔAIC >6.

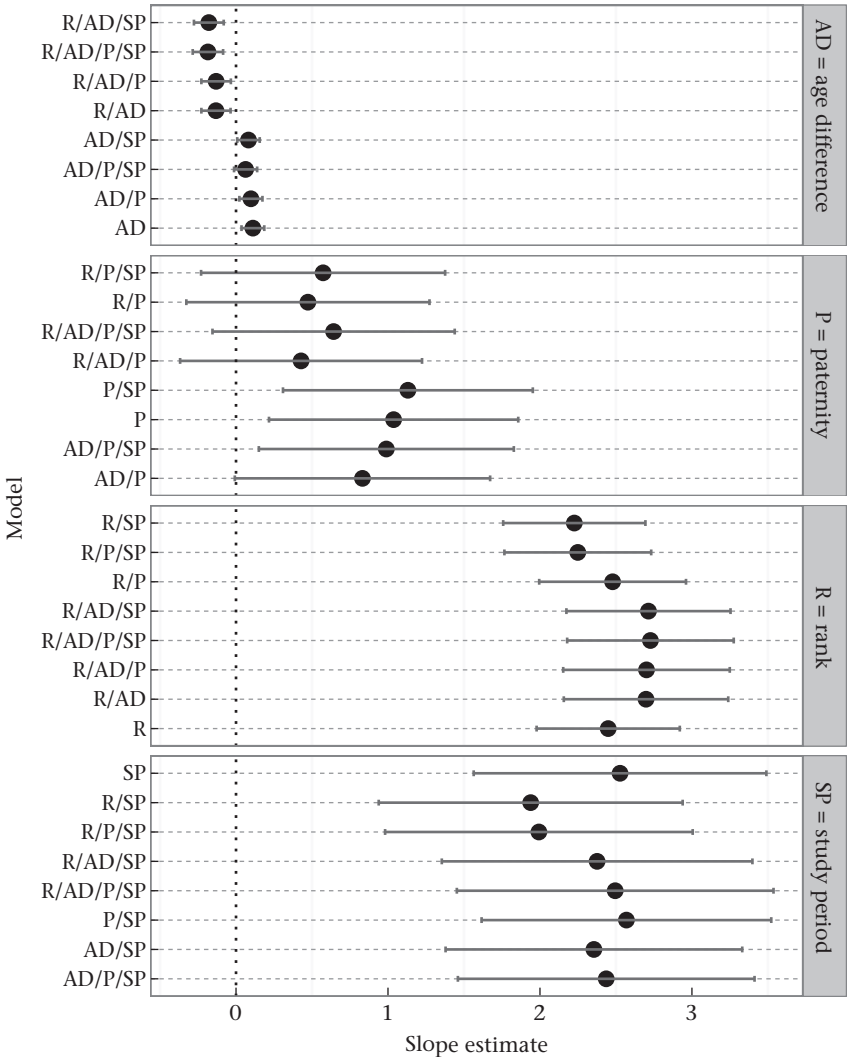

Figure 4. Estimates and standard errors for beta coefficients for each of the four predictor variables (indicated on the right) in each of the eight possible models in which the variable appeared (indicated on the left). For example, the top panel shows beta estimates and standard errors for the effect of age difference in the eight possible models in which age difference appeared as a predictor variable. Rank and study period predicted grooming/resting in contact composite measure values far better than either paternity or male–immature age difference.

Carrying and Holding

Our ad libitum and focal follow data contained 54 instances of adult males holding or carrying infants. Fifty-two instances occurred in multimale groups, and two in a single-male group. In multimale groups, males of all ranks carried and held infants. Ten males performed these behaviours, involving a total of 13 individual infants. Two alpha males accounted for 31 instances (60%), two beta males accounted for two instances (4%), one gamma male accounted for 12 instances (23%) and four subordinate males accounted for seven instances (13%). Twenty-eight of the 52 cases in multimale groups involved a father/offspring dyad, but nearly all (25) occurred within one dyad. Twenty-three other instances occurred between unrelated dyads. Paternity has not yet been determined for one infant involved in one carry.

Males tended to repeat the behaviour with certain infants. The alpha male who carried the same infant 25 times carried a similar-aged infant only once, although he was the father of both. The gamma male's 12 hold and carry behaviours were divided among only two infants (five cases with one, seven with the other) in spite of residing in a large group with many more infants available (around eight). He was not the father of either of these infants. The year after data collection ended, this male left his natal group with a splinter group that included one of these infants and its mother; the other mother/infant dyad remained in the main group.

'Fatherless' Immatures

Immatures had similar relationships with adult males in their social group regardless of whether their father was present. Comparisons of immatures whose fathers were present and immatures whose fathers were absent showed no differences in close proximity, proximity maintenance, following, resting in contact and grooming, or play. Immatures whose fathers were absent received the same amount of noncontact and contact aggression, and co-fed with males at the same rate as immatures whose fathers were present (Table 8). However, fatherless immatures received more vocal aggression and spent more time in medium proximity to males than did immatures with fathers (Table 8).

Table 5
Affiliation measures ($N = 176$ dyads)

	Model	LL	K	ΔAICc	ωAICc
Composite resting in contact+grooming	Rank[1]+study period[2] [1]β±SE=2.226±0.468 [2]β±SE=1.939±1.000	−487.39	6	0	0.32
	Rank[1]+paternity[2]+study period[3] [1]β±SE=2.249±0.483 [2]β±SE=0.573±0.803 [3]β±SE=1.993±1.012	−486.46	7	0.30	0.28
	Rank[1]+age diff[2]+study period[3] [1]β±SE=2.714±0.540 [2]β=−0.179±0.098 [3]β=2.376 SE=1.022	−487.13	7	1.65	0.14
	Rank[1]+age diff[2]+paternity[3]+study period[4] [1]β±SE=2.727±0.548 [2]β±SE=−0.185±0.100 [3]β±SE=0.642 SE=1.797 [4]β±SE=2.495 SE=1.042	−486.14	8	1.86	0.12
	Rank β±SE=2.449±0.471	−490.14	5	3.35	0.06
	Rank[1]+paternity[2] [1]β±SE=2.478±0.483 [2]β±SE=0.473±0.800	−489.28	6	3.77	0.05
Composite touching+social staring	Rank β±SE=0.697±0.163	−356.70	5	0	0.43
	Rank[1]+paternity[2] [1]β±SE=0.767±0.175 [2]β±SE=−0.410±0.377	−356.17	6	1.08	0.25
	Rank[1]+study period[2] [1]β±SE=0.684±0.164 [2]β±SE=−0.286±0.391	−356.46	6	1.65	0.19
	Rank[1]+paternity[2]+study period[3] [1]β±SE=0.753±0.177 [2]β±SE=−0.395±0.377 [3]β±SE=0.262±0.392	−355.97	7	2.84	0.10
Play	Rank β±SE=−0.0001±0.00004	1096.67	5	0	0.93

LL: log likelihood; K: number of estimated parameters; AICc: difference in adjusted AIC values; ωAICc: weight of adjusted AIC values.

Table 6
Aggression ($N = 176$ dyads)

	Model	LL	K	ΔAICc	ωAICc
Vocal aggression	Rank β±SE=0.021±0.002	472.34	5	0	0.98
Noncontact aggression	Rank β±SE=−0.005±0.001	567.87	5	0	0.98
Contact aggression	Study period β±SE=0.0021±0.0017	584.63	5	0	0.56
	Paternity β±SE=0.0011±0.0016	584.28	5	1.21	0.31
	Rank β±SE=0.0003±0.0007	583.07	5	3.12	0.12

LL: log likelihood; K: number of estimated parameters; AICc: difference in adjusted AIC values; ωAICc: weight of adjusted AIC values.

Table 7
Feeding tolerance ($N = 44$ dyads)

	Model	LL	K	ΔAICc	ωAICc
Co-feeding (2011–2012 only)	Rank β=0.013±0.004	110.00	5	0	0.96

LL: log likelihood; K: number of estimated parameters; AICc: difference in adjusted AIC values; ωAICc: weight of adjusted AIC values.

DISCUSSION

Results clearly demonstrate that social preferences of male and immature mountain gorillas are based on male dominance rank rather than paternity. Dyads that included high-ranking males spent more time near each other, actively affiliated more and fed in very close proximity more often than those containing lower-ranking males. Immatures also worked harder to maintain proximity to high-ranking males than to low-ranking males. At the same time, high-ranking males played less and directed less vocal aggression to immatures than low-ranking males did. In each case, the rate of behaviour was better predicted by male dominance rank than by paternity. High-ranking males had close ties to immatures that they had not sired. Paternity had little predictive power in any domain, strongly suggesting that males and immatures do not discriminate paternity in multimale gorilla groups. Two males also apparently failed to detect false paternity when a female emigrated into their group in the early stages of pregnancy. Because there is only one recorded instance of a female mountain gorilla successfully transferring to a new group with an infant (which, at 3 years old, was approaching weaning; Sicotte, 2000), and multiple cases of males killing infants born in their groups when females immigrated later in pregnancy, it seems unlikely that these males ignored rather than failed to detect false paternity.

The two most parsimonious explanations for why mountain gorillas failed to evolve a more sophisticated paternal kin discrimination are (1) that multimale groups were rare in the species' evolutionary history, or (2) that multimale groups occurred regularly, but reproductive skew was high enough that dominance rank was a reliable paternity cue. The finding that rank is a strong predictor of social preference supports the second scenario. If groups very rarely contained more than one adult male, then co-residence alone would be a sufficient paternity cue (e.g. Blaustein, Bekoff, & Daniels, 1987; Davies, Krebs, & West, 2012), and male–immature relationship quality might be expected to be widely distributed across all ranks of males. The strong predictive power of rank implies that immatures regularly had a choice of more than one male social partner, but rank was a very strong paternity predictor. Published paternity data from KRC's multimale groups (Bradley et al., 2005; this study, 2003–2004 data) demonstrate that reproductive skew can be quite high even when there are multiple fully adult males in a social group.

The lower skew observed in our 2011–2012 sample may be a product of natural stochastic variation, with an ageing dominant male of a large (40+) social group contributing to increased reproductive opportunities for younger, subordinate males. It is unlikely that such conditions regularly occurred in *G. beringei*'s evolutionary history; if they did, it seems probable that selection would have favoured adaptations that enhance intrasexual competition among males, such as larger testes size and faster swimming sperm. Various authors have speculated about the history of multimale, multifemale grouping in mountain gorillas and whether current conditions represent a mismatch between socio-ecological conditions of the present and the evolutionary past (e.g. Robbins et al., 2009; Robbins et al., 2013; Stoinski, Rosenbaum, et al., 2009). While groups with two males were reported as far back as the 1950s when the species was first closely observed (Schaller, 1963), groups with both the large numbers of males and high male:female ratios that were observed in the late 1990s and 2000s (Cauillaud et al., 2014; Stoinski, Rosenbaum, et al., 2009) appear to be a recent phenomenon. Our data support the notion that these groups are an evolutionarily novel configuration, although no convincing explanation for their emergence has yet been put forth.

Table 8
'Fatherless' immatures versus immatures with fathers present ($N = 193$ dyads unless otherwise noted)

Outcome variable	Predictors	β	SE	*Z*	*P*	95% CI (lower)	95% CI (upper)
Close proximity	Father presence	0.000	0.015	0.03	0.978	−0.028	0.029
	Rank	0.050	0.007	6.98	0.000	0.063	0.036
	Immature age	−0.004	0.003	1.71	0.088	−0.009	0.001
	Constant	0.205	0.028	7.39	0.000	0.151	0.260
Medium proximity	Father presence	−0.025	0.010	2.50	0.012	−0.045	−0.005
	Rank	0.025	0.004	5.79	0.000	−0.034	−0.017
	Immature age	−0.004	0.002	2.31	0.021	−0.008	−0.001
	Constant	0.150	0.018	8.57	0.000	0.116	0.184
Hinde index values (N=103 dyads)	Father presence	−0.057	0.058	0.98	0.328	−0.171	0.057
	Rank	0.096	0.018	5.22	0.000	0.132	0.060
	Immature age	0.009	0.011	0.82	0.412	−0.012	0.030
	Constant	0.368	0.083	4.43	0.000	0.205	0.531
Following (N=61 dyads)	Father presence	0.020	0.028	0.71	0.476	−0.035	0.075
	Rank	0.056	0.022	2.51	0.012	0.100	0.012
	Immature age	−0.006	0.008	0.76	0.449	−0.023	0.010
	Constant	0.182	0.069	2.64	0.008	0.047	0.317
Rest in contact/groom composite	Father presence	−0.397	1.296	0.31	0.759	−2.937	2.143
	Rank	2.072	0.447	4.64	0.000	2.948	1.197
	Immature age	0.129	0.235	0.55	0.583	−0.331	0.589
	Constant	6.644	2.041	3.26	0.001	2.644	10.644
Touch/social staring composite	Father presence	0.501	0.503	1.00	0.319	−0.484	1.486
	Rank	0.641	0.149	4.29	0.000	0.933	0.348
	Immature age	−0.219	0.092	2.39	0.017	−0.398	0.039
	Constant	2.855	0.744	3.84	0.000	1.397	4.313
Play	Father presence	0.000	0.000	0.19	0.849	−0.000	0.000
	Rank	0.000	0.000	3.18	0.001	0.000	0.000
	Immature age	0.000	0.000	0.24	0.813	−0.000	0.000
	Constant	−0.000	0.000	1.13	0.259	−0.001	0.000
Vocal aggression	Father presence	−0.012	0.005	2.18	0.029	−0.022	−0.001
	Rank	0.012	0.002	5.09	0.000	0.016	0.007
	Immature age	−0.001	0.001	0.96	0.336	−0.003	0.001
	Constant	0.053	0.009	5.67	0.000	0.034	0.071
Noncontact aggression	Father presence	0.003	0.002	1.50	0.134	−0.001	0.008
	Rank	−0.006	0.001	5.16	0.000	−0.004	−0.008
	Immature age	0.001	0.000	1.45	0.147	−0.000	0.001
	Constant	−0.019	0.005	4.06	0.000	−0.028	−0.010
Contact aggression	Father presence	0.002	0.002	0.76	0.450	−0.003	0.006
	Rank	0.000	0.001	0.31	0.756	−0.001	0.002
	Immature age	0.000	0.000	0.36	0.717	−0.001	0.001
	Constant	−0.001	0.003	0.23	0.815	−0.007	0.006
Co-feeding (N=61 dyads)	Father presence	0.008	0.005	1.50	0.134	−0.003	0.019
	Rank	0.011	0.004	2.92	0.003	0.019	0.004
	Immature age	0.001	0.002	0.37	0.710	−0.003	0.004
	Constant	0.030	0.013	2.42	0.016	0.006	0.055

Both lowland gorillas, *Gorilla gorilla*, and mountain gorillas have sexual characteristics that are on the far end of the distribution of traits associated with contest competition and single-male groups (e.g. Harcourt et al., 1981; Leutteneger & Kelly, 1977; Plavcan & van Schaik, 1997). The association between these traits and group structure is very strong, making it highly unlikely that gorillas arrived at the combination of extreme sexual dimorphism, well-developed weaponry and small testes size–body ratio via some other route. However, it is easy to conceive of this morphology developing despite a persistent minority of two-male or three-male groups with high reproductive skew, typically (although not always) made up of related males. Multimale groups may have advantages for both females and males (Robbins, 1995; Robbins et al., 2013), making it likely that these kinds of groups did not suddenly appear within the last 50 years. This population structure would produce a simple paternity discrimination algorithm that matches current data: if one male is present, associate with him; if more males are present, associate preferentially with the dominant male unless maternal cues indicate otherwise (Rosenbaum et al., 2015). Since paternal care behaviours in this species are low cost, males can afford to err on the side of infant protection even if maternal or infant cues to paternity attribution are sometimes unreliable. Selective pressure might have favoured infants who chose the dominant male as their preferred male social partner regardless of paternity, because dominant males are likely the highest-quality male and therefore the best protector. At the very least, this would not have created selection for infants to discriminate fathers from nonfathers, and at most there might actually have been selection against it. Infants who chose to affiliate with their nondominant father at the cost of forgoing superior protection by a dominant male might have been at a disadvantage, inhibiting the evolution of discrimination.

Our scenario of a species history with a persistent minority of two-male or three-male groups is further supported by two other behavioural patterns. First, immatures' collective social partner preferences map onto this structure. Even though alpha males are

the most likely father of any individual infant and most immatures prefer these males, it is notable that between 10% and 25% of immatures prefer their group's beta male to the alpha (Rosenbaum, Hirwa, Silk, Vigilant, & Stoinski, 2015; Rosenbaum, Silk, & Stoinski, 2011; Stewart, 2001). This is similar to the percentage of nonalpha sirings both in Bradley et al.'s (2005) data from the 1990s and more recent data. This suggests a form of behavioural bet hedging, similar to the behavioural patterns observed in chacma baboons when females are lactating (Moscovice et al., 2010). Second, an evolutionary history that regularly included two-male groups might help explain the remarkable behavioural flexibility Karisoke's mountain gorillas have demonstrated in the last 20 years. For a species with such extreme morphological adaptations for contest competition to abruptly shift to a promiscuous social system suggests that male gorillas' behavioural repertoire included tolerance of, and occasional cooperation with, other adult males.

Besides rank, the other notable predictor of our behavioural measures was study period; dyad partners in the 2011–2012 sample spent more time near each other, actively affiliated more and engaged in less contact aggression than the dyads observed in 2003–2004. It is more likely that these differences were due to differences in group size or male:immature ratio than to differences in reproductive skew across the two study periods. Smaller groups tend to be less spread out (S. Rosenbaum, personal observations) and move less frequently (Ganas & Robbin, 2005), providing more opportunity for close proximity and active affiliation. Also, the ratio of immature:dominant males (i.e. the most preferred males) was much higher in 2003–2004. Because space near a single male was limited, immatures in 2003–2004 may have been constrained by competition with their peers. In large groups, male attention and proximity might be viewed as a limited resource over which immature animals compete. More work is needed to determine whether such competition motivates the social preferences of the minority of immatures who prefer nondominant males.

The paternity data presented here also provide further support for current theories of reproductive skew in mountain gorillas. Stoinski, Rosenbaum, et al. (2009) found support for a concessions model based on mating behaviour, but lacked genetic paternity data. Our 2003–2004 sample had, on average, 13 more animals per group than the 2011–2012 sample, and the group from this period with the smallest number of males (six) had more than the group with the largest number of males (five) in 2011–2012 (see Table 1). Such demographic differences should have made dominant male 'policing' of females and nondominant males much harder in 2003–2004 than in 2011–2012. However, in spite of this, dominant males' reproductive success was much higher in the earlier sample. This suggests that dominant males' reproductive success was not constrained by their inability to exclude other males.

The lack of paternal kin discrimination in mountain gorillas is an informative case study of both remarkable social flexibility and evolutionary limitations. Paternal kin discrimination is now well established in a variety of primate species with multimale, multifemale social systems. While gorillas are clearly able to adopt the social structure of such species, an important mechanism underlying kin selection is apparently absent. This provides an interesting opportunity to track fitness outcomes associated with changes in social structure over the coming years and to test predictions about the outcomes of evolutionarily novel social environments.

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