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Relationships Between Adult Male and Maturing Mountain Gorillas (*Gorilla beringei beringei*) Persist Across Developmental Stages and Social Upheaval

Stacy Rosenbaum*, Jean Paul Hirwa†, Joan B. Silk‡§ & Tara S. Stoinski¶

* Department of Anthropology, University of California-Los Angeles, Los Angeles, CA, USA
† Dian Fossey Gorilla Fund International, Musanze, Rwanda
‡ School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA
§ Institute of Human Origins, Arizona State University, Tempe, AZ, USA
¶ Dian Fossey Gorilla Fund International, Atlanta, GA, USA

Correspondence
Stacy Rosenbaum, Institute for Mind and Biology, University of Chicago, 940 E 57th Street, Chicago, IL 60637, USA.
E-mail: srosenbaum@uchicago.edu

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Abstract

Across the animal kingdom, long-term social relationships outside the context of reproductive pair bonds are rare. However, they have been demonstrated in some mammals including primates, cetaceans, and social carnivores. The ontogeny of such relationships is likely to depend on the benefits individuals can gain by cultivating them. Previous studies demonstrated that young mountain gorillas (*Gorilla beringei beringei*) have strong relationships with adult males, but little is known about the longevity of these bonds. Here, we examine the temporal stability of proximity relationships between coresident adult male and maturing gorillas in the habituated population monitored by the Dian Fossey Gorilla Fund International's Karisoke Research Center in Volcanoes National Park, Rwanda. We used spatial proximity data to assess the strength of relationships between adult males and juveniles, and tracked these relationships as the juveniles matured into subadults (3–4 yr later; n = 229 dyads) and then young adults (7 yr later; n = 42 dyads). The proximity relationships of juveniles of both sexes predicted their proximity relationships with adult males in both subadulthood and young adulthood. However some young adult males who had lost their top adult male proximity partner from juvenilehood developed new relationships with older males that had risen in the dominance hierarchy. These data suggest that (1) kin selection may play a more important role in social relationships between potential fathers and adult female offspring than previously suspected, and (2) when maturing males' foremost adult male social partners remain available to them, their relationships can be stable past the age at which younger males become reproductive competitors.

Introduction

Social animals are expected to invest in relationships that provide fitness benefits (Kummer 1978). The benefits that animals derive from intra- and intersex social bonds depend on the species' ecology and social structure. In some socially monogamous species, investment in long-term reproductive pair bonds increases offspring quality and survival (e.g., mice: Gubernick & Teferi 2000; snapping shrimp: Mathews 2002; coral-dwelling gobies: Wong et al. 2008; songbirds: Matysioková & Remeš 2013; mimic poison frog: Tumulty et al. 2013). In many gregarious species, relationships with partners other than mates have important fitness consequences as well. Social partners enhance access to food (chimpanzees: Mitani & Watts 2001), increase social status (macaques: Schülke et al. 2010; Berghänel et al. 2011), provide reproductive opportunities (dolphins: Connor et al. 1992), and offer social information or support/protection (lions:

Packer & Pusey 1983; coatis: Russell 1983; elephants: McComb et al. 2001; baboons: Silk et al. 2009). In some instances, the quality of non-reproductive social relationships influences fitness outcomes (e.g., baboons: reviewed in Silk 2007; wild horses: Cameron et al. 2009; dolphins: Frère et al. 2010; Assamese macaques: Schülke et al. 2010).

The utility of social relationships with particular partners can change over time. Maturation, changes in social or reproductive status, or changes in group structure may increase or decrease the value of individual social partners. For example, male–female 'friendships' in chacma baboons are terminated after the death of a nursing infant (Palombit et al. 1997), and 'helpers at the nest' can become too numerous and begin competing with breeding animals (e.g., banded mongoose: Cant et al. 2001). Changes in the value of social partners are likely to be most common when individuals spend extended periods of time in the same social group. Sex-biased dispersal, common in mammals and birds, limits the potential for development of long-term social relationships with certain categories of social partners who might be valuable allies (reviewed in Dobson 2013). For example, orphaned female chacma baboons receive valuable support from their older maternal brothers, but males in this species typically disperse when they reach sexual maturity (Engh et al. 2009).

Mountain gorillas (*Gorilla beringei beringei*) provide an important opportunity to investigate the temporal changes in social relationships for two reasons. First, they have a flexible social system in which both sexes often mature and reproduce in their natal group (Harcourt et al. 1976; Watts 2000). In the longest monitored population, approximately 60% of females reproduce in their natal group (Robbins et al. 2009a). Fifty percent of males remain in their natal groups and those that do disperse rarely leave before they become full silverbacks (i.e. adult males 12–14 yr, Watts & Pusey 1993; Stoinski et al. 2009a). Second, tenure of alpha males can be long, up to 19 yr (Karisoke Research Center long-term records; maximum life expectancy for the species in the wild is ~30–35 for males (median = 23) and ~35–40 for females (median = 33); Bronikowski et al. 2011). Although relationships between males and immatures are generally strong, alpha males form particularly strong bonds with immatures regardless of whether they are the genetic father (Stewart 2001; Rosenbaum et al. 2015). As immature males age, however, adult males who once provided protection from infanticide (Watts 1989; Robbins et al. 2013) and displayed high levels of social tolerance (Stewart 2001; Rosenbaum et al. 2011) may become rivals for top social positions, or allies in attaining high rank. Adult males may also present inbreeding hazards for maturing females. These features of mountain gorilla social groups allow us to track social bonds across time, and to investigate possible reasons for changes in the strength of relationships as immatures mature.

The modal social structure for *Gorilla beringei* consists of one or more females and their young, who associate permanently with a single adult male (i.e., a harem structure). However, because male gorillas often do not disperse, approximately 40% of the gorilla groups in the Virunga massif (which contains 54% of the world's extant population and is one of only two remaining habitats) now contain multiple adult males (mean = 3.2, range = 2–8; Weber & Vedder 1983; Gray et al. 2010). For 9 yr, the social groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center all included multiple adult males and multiple adult females (hereafter referred to as multimale groups) and were remarkably large. From 2000 to 2007, social group size ranged from 22 to 65 individuals (mean = 33.3 animals per group), with at least four silverbacks in each of the three monitored groups. Our previous work determined that the adult males in these large multimale groups formed close relationships with immatures (Rosenbaum et al. 2011) and that male dominance rank was a far better predictor of relationship strength than either genetic paternity or age difference between the male and immature (Rosenbaum et al. 2015). While alpha males are the most likely father of any given infant, there can be considerable variation in reproductive skew in this population, and non-dominant males regularly sire infants (Rosenbaum et al. 2015; Vigilant et al. 2015). Currently, nothing is known about the trajectory of relationships between adult males and maturing animals in their groups as the younger social partners mature and social dynamics change.

The goal of this study was to evaluate the temporal stability of relationships between adult male and maturing gorillas in multimale groups. Immatures of both sexes spend progressively more time in close proximity to non-dominant males from ages 3 to 6 (Rosenbaum et al. 2011), suggesting that immatures may systematically alter their proximity relationships with adult males as they mature. Harcourt & Stewart (1981) noted that young adult males were less likely to disperse from their natal group if the dominant male at the time of their birth was still dominant, but their observations were based on a sample of only four young males. Maternal absence is a predictor of adult male dispersal (Stoinski et al. 2009a), which suggests that maturing animals may sustain important relationships from their infancy long past weaning. However, the stability of relationships between adult male and maturing mountain gorillas has not been systematically evaluated.

We predicted that proximity relationships between maturing males and adult males would be more stable than proximity relationships between maturing females and adult males, did, for three reasons. First, males are unable to transfer between established social groups, but females are. Thus, the primary path for a male to reside in a multimale group is to remain in his own natal group (Robbins 1995). There are benefits to living in multimale groups, including better infant survival and female retention (e.g., Watts 1989; Sicotte 1993; Robbins 1995; but see also Robbins et al. 2013) plus potential for queuing for dominance (Robbins & Robbins 2005) and its associated reproductive benefits. Thus, both maturing and fully adult males could profit from developing and maintaining tolerant relationships with one another. Second, females who remain in their natal groups after sexual maturity may be motivated to distance themselves from males who are old enough to be their fathers to avoid inbreeding. Proximity avoidance could potentially work as a proximate mechanism for inbreeding avoidance in species where non-sex-biased dispersal necessitates other measures (e.g., capuchins: Muniz et al. 2006). Third, long-term relationships between adult males and females are rare outside the context of mating.

It is unclear whether to expect the importance of adult male rank in predicting relationships to wane as immature gorillas age. The utility of such relationships is clear when they are young; the alpha male is the most likely father (Bradley et al. 2005; Rosenbaum et al. 2015; Vigilant et al. 2015) and an important source of protection against infanticide (e.g., Watts 1989; Robbins et al. 2013). As infants mature and their need for protection decreases, the benefits of a close relationship with the alpha male (who is most infant's closest adult male social partner; Stewart 2001; Rosenbaum et al. 2011) may decrease for both parties. However, it may be useful for gorillas to maintain these relationships as young animals mature for other reasons. Support from subadult/young adult males may help alpha males maintain their dominance if they face challenges from other males. For subadult/young adult males, a relationship with the dominant male may help ensure access to females who generally cluster around the dominant male (Harcourt 1979; but see also Stoinski et al. 2009a) or improve their chances of eventually attaining top dominance rank themselves. For females who are approaching reproductive maturity, a relationship with the dominant male could provide mating opportunities with a high-quality male if he is not her father, or protection for her infants if he is.

Methods

Subjects and Data Collection

This study used data collected on the habituated mountain gorilla population monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center (KRC) in Volcanoes National Park, Rwanda, between January 2004 and December 2011. Data were extracted from the KRC long-term database, which includes information on proximity collected via instantaneous point sampling during focal animal follows for all animals over 1 yr of age. Every 10 min, researchers recorded the identity of all animals within a 2-m radius of the focal animal. Data were collected by a variety of observers who passed repeated interobserver reliability tests.

Data analyzed here were collected in all months of 2004, 2007, and 2011. These years were chosen because data collection by the first author (in 2004 and 2011), second author (in 2011), and a complimentary research project (in 2007) maximized the available proximity data for adult male and maturing partner dyads. The sample included all adult male and maturing gorillas living in the habituated KRC population who were coresident in a social group for (1) at least two of the three analyzed years and (2) at least 5 mo in each of the years the dyad was analyzed. Five months typically corresponded to our minimum required 10 h of focal follow data per dyad. We eliminated dyads not coresident for at least 5 mo to minimize the possibility that short-term stochasticity in partner preference would bias results. The sample consisted of 229 dyads made up of an adult male and a maturing partner. In total, this included 21 adult males and 44 maturing partners (26 males, 18 females). During the first year of the data collection period, maturing animals ranged in age from 1 to 5 yr; by the end, the oldest were 12 yr of age.

During the 7-yr time span considered here, there was significant social upheaval in the study groups. This included the death of two dominant and one 3rd-ranked male; the rank switch of a dominant and 2nd ranked male; the return of a low-ranking male to his natal group after a 3-yr absence; and group fissions that eventually split three social groups into nine. Five of the nine are considered here; there was insufficient data available in a 6th, and the others did not contain dyads of the relevant demographic. Figure 1 summarizes available dyad partners across time for the animals included in these analyses. Changes in group name signify group fissions. The number of dyads decreases across time as subjects died, dispersed, or were separated after group splits. See Caillaud et al. (2014) for complete demographic details of the KRC population.

Measuring Social Relationships

To measure social relationships, we used information about the proportion of time social partners spent in close proximity to one another. Following a number of previous studies of gorillas, we defined close proximity as <2 m (e.g., Watts 1992, 1994; Nakamichi & Kato 2001; Stoinski et al. 2003). Across species, proximity is generally correlated with other measures of affiliation (e.g., grooming in baboons: Silk et al. 2003; grooming, muzzle contact, and affiliative contact in mandrills: Charpentier et al. 2007; allogrooming in feral horses: Cameron et al. 2009), so proximity patterns are used to infer tolerance and closeness (e.g., sperm whales: Gero et al. 2008; giraffes: Carter et al. 2013; big brown bats: Kilgour et al. 2013). For gorillas, maternal relatives and longer term social partners (i.e., natal residents) spend more time in proximity to one another than to unrelated animals or new immigrants (Watts 1992, 1994). Avoidance of close proximity may be used to deter aggression, particularly for male gorillas (e.g., Robbins 1996), and initiating or maintaining close proximity is a primary reconciliation mechanism in western lowland gorillas (Mallavarapu et al. 2006). Moreover, proximity is less likely to be strongly influenced by developmental stage or sex than other behavioral measures, such as play and grooming which change in frequency with age (Meder 1990; Maestripieri & Ross 2004; Rosenbaum et al. 2011). This is important because we are interested in evaluating the changes in social relationships across developmental stages.

Categorization of Age/Sex Classes

Our analyses were based on data collected during three time periods: 2004, 2007, and 2011. Males that were at least 8 yr old in 2004 were classified as adults. Although males do not reach full adulthood until they are 12–14 yr of age (Watts & Pusey 1993), they begin exhibiting important forms of adult behavior, including copulations, siring infants, and participating in intergroup interactions, by the age of eight (Robbins 1995; Vigilant et al. 2015; KRC long-term records).

During each time period, we categorized the maturing partner in each adult male–maturing partner dyad into one of three developmental categories: juveniles, subadults, and young adults. Individuals that were 1–5 yr old in 2004 were categorized as juveniles in the first time period (mean age = 3.30 yr, SD = 1.42, n = 44), as subadults during the second period (mean = 6.42, SD = 1.41, n = 41), and as young adults in the third period (mean = 10.02, SD = 1.64, n = 22). Similarly, animals that were 1–5 yr old during the second time period were categorized as juveniles during that time period, and subadults in the

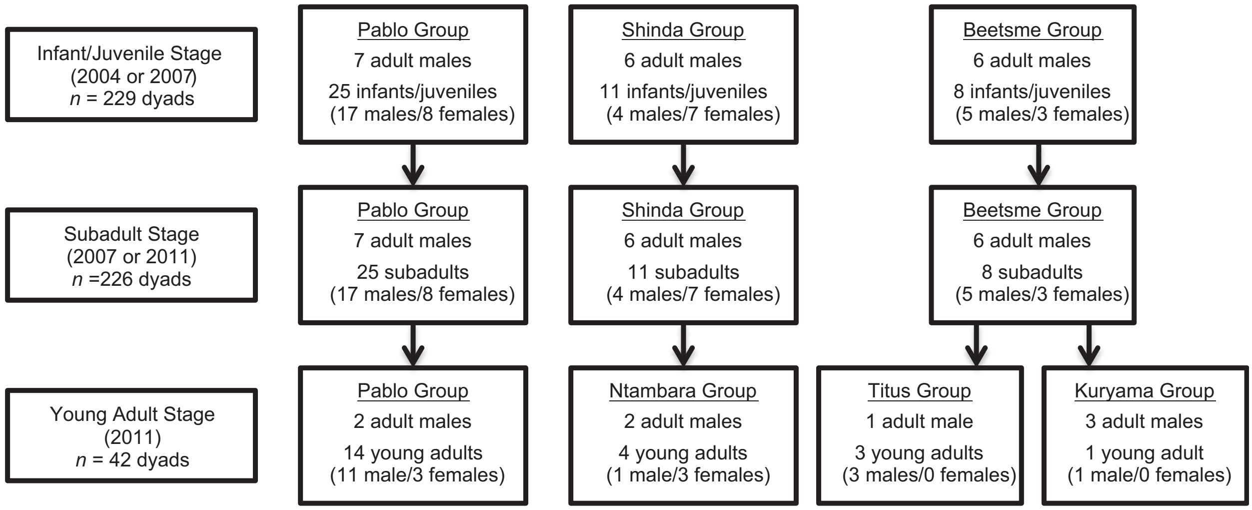

Fig. 1: Sample sizes and social structure progression across the three developmental stages for maturing gorillas in each adult male–maturing partner dyad. Counts include only adult males and maturing partners in each social group, and do not reflect presence of other group members (e.g., adult females) not included in the present analyses.

third period (Fig. 1). The classifications juvenile, subadult, and young adult roughly follow the developmental stages for this species outlined in Watts & Pusey (1993), but here are also used as shorthand to concisely distinguish youngest/middle/oldest age categories of the maturing partner. We use the terms 'adult male partner' and 'maturing partner' throughout to distinguish animals who entered the dataset when they were juveniles (the maturing partner) vs. those who entered the data set as (8+)-yr-old males (the adult male partner).

Dominance Rank

Adult males were assigned ranks based on nonaggressive displacement patterns using methods described in Stoinski et al. (2009b). Male ranks were assessed in each time period. In one group, the alpha and beta male switched ranks during 2007 (D. Caillaud pers. comm., KRC long-term records). This rank change occurred early in the year, so these two males were assigned the ranks that they held for the majority of the year. We were unable to accurately determine specific rank below position three in most cases, so males ranked lower than third are categorized as 'subordinate'.

Kinship

Maternal kinship of all natal individuals was known from long-term observation at KRC. Thirteen dyads were composed of maternal siblings (n = 4 adult male–maturing male dyads, 9 adult male–maturing female dyads). All of the sibling dyads were observed in the juvenile and subadult stages; only two sibling dyads were still coresident during the young adult stage. The strength of sibling relationships may be influenced by their age difference (S. Rosenbaum & T.S. Stoinski, unpub data), so we tested whether sibling and non-sibling dyads had similar age gaps. There was no difference in the age difference of sibling and non-sibling dyads (random effects ANOVA: $\beta = 1.88$, SE = 2.17, Z = 0.87, p = 0.39), and both types of dyads spent similar amounts of time together across developmental stages (siblings: mean = 5.1%, SD = 3.4%; non-siblings: mean = 4.7%, SD = 5.5%).

For one analysis, we divided adult male partners into genetic fathers and non-fathers, to specifically address whether maturing females and genetic fathers distance themselves (relative to maturing females and unrelated adult males) as females reach sexual maturity to avoid inbreeding. In one case, a female's father was also her maternal brother.

The paternity information used here represents a subset of a larger set of paternity assessments described in detail in Vigilant et al. (2015). Fecal samples were collected from infants, mothers and all potential fathers for non-invasive analysis. Samples were preserved using methods described in Nsubuga et al. (2004), and genotyped at 16 autosomal microsatellite loci using methods detailed in Arandjelovic et al. (2010). Individual animal's sample identifications were confirmed by comparing at least two samples purported to be from the same individual, or from known mother/infant pair genotypes. All resident males at least 7 yr old when the infant was conceived were considered possible sires. Paternity likelihood assessment was conducted using CERVUS 3.0.3 (Kalinowski et al. 2007). CERVUS had to assign sires with 95% confidence to be included in the dataset. In addition to CERVUS statistical confidence, mother, infant, and potential sire genotypes were compared for genotypic incompatibilities ('mismatches').

Data Summary and Analysis

Proximity data, collected as instantaneous point samples, were derived from 50-min focal follows of both adult males and maturing partners. For each dyad, the two partners had a minimum of 72 instantaneous proximity point samples, which equals 10 h of focal follow data (per dyad, in 2004 mean = 235.2 point samples, range = 72–642; 2007: mean = 367.6 point samples, range = 79–895; 2011: mean = 678 point samples, range = 85–1000). For each year, we summed the number of point samples in which one dyad partner appeared within 2 m of the other and divided that by the total number of point samples available for both dyad partners, to obtain a proportion of samples in which the dyad partners were in close proximity to one another.

A considerable percentage of dyads during each time period involved subordinate adult males (e.g., 144 of 220 dyads in 2004). Subordinate males generally spend much less time with maturing animals than higher ranking males do (e.g., Rosenbaum et al. 2011). This means that the inclusion of subordinate males may artificially amplify the effects of rank. Therefore, some analyses were restricted to only dyads including males that held the top three ranks.

The unit of analysis was the dyad. To assess predictors related to our outcome variable, proximity relationship strength, we used multilevel, mixed effects linear regression models. To control for the repetition of individuals across dyads, we included the IDs of each dyad partner as random effects variables in all models. We used the same basic mixed effects structure for all models.

Previous work indicated that some potentially relevant predictors of relationship strength in adult male–maturing partner dyads (specifically, the age difference between the dyad partners, and paternity) did not predict relationship strength (Rosenbaum et al. 2015). Therefore, we limited the predictor variables in our models to those directly relevant to our predictions (juvenile stage proximity relationship, maturing partner sex) and the variable well established as a significant predictor of such relationships (male rank). We used standard hypothesis testing methods to determine how these predictors were related to proximity relationship strength at each developmental period.

For each developmental period (juvenile, subadult, young adult), we ran a basic model that contained each of the predictors as a main effect (though for the juvenile stage outcome variable, only rank and sex were included as no earlier developmental stage was available). To evaluate the predictive power of our basic candidate models, we compared each of these models to a null model containing only the random effects using difference of adjusted Akaike information criteria values (ΔAICc; Anderson & Burnham 2002; McElreath et al. 2008). For the models in the juvenile, subadult, and young adult developmental stages (Tables 1a, 2a, and 3a), the ΔAICc for the nulls were 120.98, 90.92, and 10.34, respectively. Differences of >2 are generally considered meaningful, indicating there was substantial support for the candidate models over the null models. Based on the output of the models and visual inspection, we then tested models with interaction effects and/or additional predictors for the later two developmental stages. The model(s) tested for each developmental stage are described below.

Juvenile Stage Proximity Relationships

For the juvenile stage proximity relationship data, we ran a model containing the predictors male dominance rank (0 = alpha, 1 = beta, 2 = gamma, 3 = subordinate) and maturing partner sex (0 = male, 1 = female), to replicate previously published results (e.g., Rosenbaum et al. 2011) demonstrating that (1) male dominance rank was a strong predictor of proximity relationships, and (2) there was no sex difference in proximity relationships at this developmental stage.

Table 1: (a) At the juvenile stage, dyads that included higher ranking adult males spent more time in close proximity than dyads containing lower ranking adult males. Sex of the juvenile partner did not predict time dyads spent in close proximity (all dyads, n = 229). (b) The results were the same when dyads containing subordinate males (<gamma rank) were removed from the analyses (dyads with top 3 ranked males only, n = 80).

Juvenile stage	Coef.	Std. Err.	Z	p	95% CI (lower)	95% CI (upper)
(a)						
Rank	−0.033	0.004	−9.21	**0.000**	−0.040	−0.026
Sex	0.003	0.006	0.48	0.632	−0.009	0.015
Constant	0.149	0.012	11.97	**0.000**	0.125	0.174
(b)						
Rank	−0.051	0.014	−3.62	**0.000**	−0.078	−0.023
Sex	0.009	0.017	0.52	0.602	−0.024	0.041
Constant	0.172	0.025	6.78	0.000	0.122	0.221

Table 2: (a) At the subadult stage, proximity relationships were strongest for dyads that (1) contained high-ranking adult males; (2) contained subadult males rather than females; and (3) had strong proximity relationships in the juvenile stage (all dyads, n = 226). (b) When dyads containing subordinate adult males (<gamma rank) were removed from the model, there was still a weak trend for adult male–subadult male dyads to have stronger proximity relationships than adult male–subadult female dyads (dyads with top 3 ranked males only, n = 99). (c) Results suggested juvenile stage proximity relationships predicted subadult stage proximity relationships better for adult male–subadult male dyads than adult male–subadult female dyads (p < 0.1) (all dyads, n = 226).

Subadult stage	Coef.	Std. Err.	Z	p	95% CI (lower)	95% CI (upper)
(a)						
Rank	−0.015	0.005	−3.04	**0.002**	−0.025	−0.005
Sex	−0.021	0.010	−2.14	**0.032**	−0.041	−0.002
Juvenile stage	0.515	0.071	7.21	**0.000**	0.375	0.655
Constant	0.084	0.018	4.69	0.000	0.049	0.119
(b)						
Rank	−0.048	0.015	−3.08	**0.002**	−0.078	−0.017
Sex	−0.025	0.015	−1.65	*0.099*	−0.054	0.005
Juvenile stage	0.497	0.086	5.78	**0.000**	0.329	0.666
Constant	0.138	0.034	4.11	0.000	0.072	0.204
(c)						
Rank	−0.014	0.005	−2.94	**0.003**	−0.024	−0.005
Sex	−0.011	0.012	−0.97	0.330	−0.034	0.011
Juvenile stage	0.613	0.089	6.89	**0.000**	0.439	0.788
Sex × Juv stage	−0.195	0.108	−1.80	*0.072*	−0.407	0.017
Constant	0.077	0.018	4.31	0.000	0.042	0.113

Subadult Stage Proximity Relationships

We ran an identically structured model with the subadult developmental stage proximity relationship data as the outcome variable. In addition to adult male rank and maturing partner sex, we included juvenile

Table 3: (a) In the young adult stage, adult male–young adult female dyads spent more time in close proximity than adult male–young adult male dyads [all dyads (no subordinate males remaining), n = 42]; (b) Juvenile stage proximity relationships predicted young adult stage proximity relationships for adult male–young adult female dyads, but not for adult male–young adult male dyads [all dyads (no subordinate males remaining), n = 42]; (c) When clustered outlier dyads containing adult male–young adult male dyads were removed (Fig. 4), juvenile stage proximity relationships predicted young adult stage proximity relationships for both sexes [outlier dyads from Fig. 4 removed (no subordinate males remaining), n = 38].

Young adult stage	Coef.	Std. Err.	Z	p	95% CI (lower)	95% CI (upper)
(a)						
Rank[a]	−0.018	0.018	−0.97	0.332	−0.053	0.018
Sex	0.037	0.013	2.80	**0.005**	0.011	0.064
Juvenile stage	0.207	0.125	1.66	*0.098*	−0.038	0.453
Juv pref partner presence	−0.009	0.014	−0.66	0.509	−0.037	0.019
Constant	0.073	0.030	2.46	0.014	0.015	0.131
(b)						
Rank[a]	−0.013	0.021	−0.62	0.537	−0.053	0.028
Sex	0.002	0.017	0.09	0.929	−0.032	0.035
Juvenile stage	0.128	0.111	1.15	0.251	−0.090	0.346
Sex × Juvenile stage	0.750	0.271	2.77	**0.006**	0.219	1.281
Constant	0.071	0.034	2.08	0.037	0.004	0.137
(c)						
Rank[a]	0.006	0.014	0.40	0.688	−0.022	0.033
Sex	0.021	0.013	1.64	0.101	−0.004	0.045
Juvenile stage	0.206	0.080	2.58	**0.010**	0.050	0.362
Sex × Juvenile stage	0.641	0.205	3.12	**0.002**	0.238	1.043
Constant	0.017	0.024	0.72	0.474	−0.029	0.063

[a] Data included a single dyad containing a gamma male; the adult males in all other dyads held alpha or beta dominance ranks.

stage proximity relationships as a predicator variable, to test whether proximity relationships at the maturing partners' juvenile stage predicted proximity relationships at the subadult stage. We retained maturing partner sex as a predictor to test the sex-specific predictions outlined above. We retained male rank because it is well established to be the primary predictor of relationship strength between adult males and juveniles (e.g., Stewart 2001; Rosenbaum et al. 2011, 2015) and is likely to continue playing an important (though perhaps diminishing) role as maturing animals age.

Based on model output and visual inspection, we then tested an additional model with an added juvenile stage × maturing partner sex interaction term. We used ΔAICc values to determine whether the model containing the interaction term better fit the data than the original model containing only the primary effects. In cases where the ΔAICc was <2, we also calculated AICc weights (ωAICc). Weights can be interpreted as the likelihood that the given model is the best choice among the candidate models tested (Anderson & Burnham 2002; e.g., House et al. 2013).

By definition all maturing animals had all their adult male social partners available to them in at least one developmental stage after juvenilehood, so we also calculated the percent of maturing animals whose top adult male partner from the juvenile stage remained the adult male they had the strongest proximity relationship with as a subadult. Proximity relationship distributions tend to be unimodal for this demographic (that is, a relationship with one adult male is much stronger than all others for each maturing partner; Rosenbaum et al. 2011), so this percentage provides an estimate of the stability of the most important relationship from the juvenile stage.

For the maturing partners who had different top adult male partners in the juvenile and subadult stages, we calculated the mean drop in former top male social partners' place in the hierarchy of subadults' proximity relationships. For example, if an adult male a maturing animal had the strongest proximity relationship with as a juvenile was the adult male they had the 3rd strongest relationship with as a subadult, the stability measure associated with that subadult would be -2. If the maturing partner had equally strong proximity relationships with two or more adult males, they all received the same rank in the subadult's proximity relationship hierarchy. We then aggregated the amount that formerly top-ranked adult male partners dropped in the subadults' male social partner hierarchy. Not all maturing partners had the same number of males available, and thus, it was possible for some former top partners to fall further in the hierarchy than others, so we also report the mean number of hierarchy spots subadults had. As more than one adult male could occupy the same spot, this is not necessarily equivalent to the number of adult male social partners. This measure is only provided at the subadult stage. By young adulthood, many maturing animals no longer had the majority of their juvenile stage partners available to them (including former top-ranked partners), so this was no longer a meaningful measure of change.

Young Adult Stage Proximity Relationships

For the young adult stage, we added a fourth main effect to the basic candidate model described above. We included the presence/absence of the maturing partner's most preferred adult male partner from the juvenile stage (0 = absent, 1 = present) where indicated, because visual inspection suggested different patterns for maturing animals who did and did not have these males present. We also tested a model containing a sex × juvenile stage proximity relationship interaction effect, as for the subadult stage, and again compared models with/without the interaction term via ΔAICc values. Addition or removal of the interaction effect and/or the presence/absence of the preferred adult male partner are reported in the text of the results and tables (Table 3a–c). Finally, visual inspection indicated a cluster of outliers in the adult male–maturing male data. We tested the young adult stage models both with and without the cluster of outliers included (Table 3b,c). Each data point is presented graphically (Fig. 4) so the reader can determine exactly what was removed.

Inbreeding Avoidance Prediction

We constructed one additional model to specifically evaluate whether father–daughter dyads spent less time together relative to unrelated dyads once the females had reached sexual maturity (the young adult stage). This was an important component of our prediction that adult male–maturing female proximity relationships would be less stable than adult male–maturing male proximity relationships. We used genetic paternity and male rank as fixed effects, and animal identities as random effects. As stated above, genetic paternity was excluded from the other models because previous work indicated it was not a meaningful predictor of such relationships (Rosenbaum et al. 2015). However, as inbreeding avoidance may be a domain in which kin discrimination is particularly important, we included it in this model to determine whether it was related to proximity relationships in the pairs (i.e., adult males and females old enough to conceive) where inbreeding could occur.

The sample size varied across analyses as animals moved in and out of the sample due to death, dispersal, and specific requirements for analyses, so the n is reported for each analysis in the relevant table. All statistical analyses were performed using Stata 13 (StataCorp, College Station, TX, USA).

Results

Proximity Relationships of Juveniles and Adult Males

As in previous studies, dyads containing higher ranking adult males spent more time in close proximity than dyads containing lower ranking adult males (Table 1a). When we restricted the analysis to dyads including the three highest ranking males, the same pattern held (Table 1b). Sex of the juvenile partner had no effect on proximity relationships with adult males (Table 1a,b).

Proximity Relationships of Subadults and Adult Males

The proximity relationships of adult male–juvenile dyads predicted the proximity relationships of adult male–subadult dyads (Table 2a). That is, dyads that spent a large proportion of time in close proximity when the maturing partner was a juvenile continued to spend a lot of time in close proximity when the maturing partner was a subadult. As in the juvenile stage, dyads containing high-ranking adult males had stronger proximity relationships than dyads containing low-ranking adult males (Table 2a). Adult male–subadult male dyads spent more time in close proximity than did adult male–subadult female dyads (Table 2a), but this difference was reduced ($p < 0.1$) when the analysis was restricted to dyads including the three top-ranking adult males (Table 2b).

A juvenile stage × maturing partner sex interaction term was then added to the model (Table 2c). Adult male–juvenile proximity relationships predicted adult male–subadult proximity relationships for both sexes, but this pattern tended to be stronger when the maturing partner was male (simple slope for males: 0.614; for females: 0.419; $p = 0.072$; Fig. 2). AICc scores for models with and without the interaction term were similar, with an ΔAICc of 0.92. AICc weights suggested that the model with the interaction term (ωAICc = 0.61) was a better choice than the model containing only main effects (ωAICc = 0.39).

Twenty-eight of the 44 subadults (64%) had the strongest proximity relationship with the same adult male they had the strongest relationship with when they were a juvenile. The other 16 had a stronger proximity relationship with a different male at the subadult stage. For those animals, on average their former top partners dropped 1.44 places (SD = 0.63, min = −1, max = −3) in the subadult partners' hierarchy of adult male social partners. The mean number of possible hierarchy slots was 4.5 (SD = 1.63, min = 2, max = 7).

Proximity Relationships of Young Adults and Adult Males

As maturing gorillas reached the young adult stage, many of the adult males that they had lived with as juveniles were no longer in their social groups. Only 22 of the gorillas that we observed as juveniles (50%

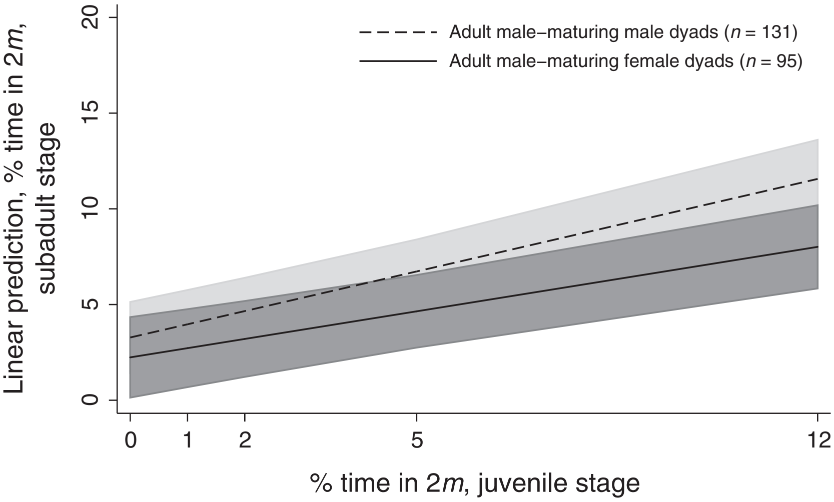

Fig. 2: Juvenile stage proximity relationships trended toward predicting subadult stage proximity relationships better for adult male–maturing male dyads than adult male–maturing female dyads ($p < 0.1$). Plot of the conditional marginals, with *x*-axis ticks representing the 10th, 25th, 50th, 75th, and 90th percentiles of time in close proximity values for all adult male–juvenile partner dyads. Shaded areas are 95% confidence intervals for prediction lines.

of the maturing animals, representing 19% of the original dyads) and as young adults still lived with at least one of the adult males they had lived with as juveniles. Half of these individuals still lived with the adult male that they had spent the most time in close proximity to as a juvenile. These adult males are referred to as 'top juvenile proximity partners' hereafter. The presence of a young adult's top juvenile proximity partner did not predict the total proportion of time the young adult spent in close proximity to adult male partners (top juvenile proximity partner present: mean = 0.04, SD = 0.04, range = 0.00 to 0.13, n = 23 dyads; top juvenile proximity partner absent: mean = 0.06, SD = 0.05, range = 0.00 to 0.16, n = 19 dyads; z = 0.35, p = 0.727; Fig. 3). This suggested that individuals whose top juvenile proximity partner was no longer present increased the amount of time they spent close to other males.

Visual inspection of the data suggested that maturing females and males went about this in different ways. For maturing females, there was a clear association between their proximity relationships as juveniles and young adults (Fig. 4; simple slope = 0.878). Females who had lost their top juvenile proximity partner increased the amount of time that they spent with secondary partners, but did not form close ties to

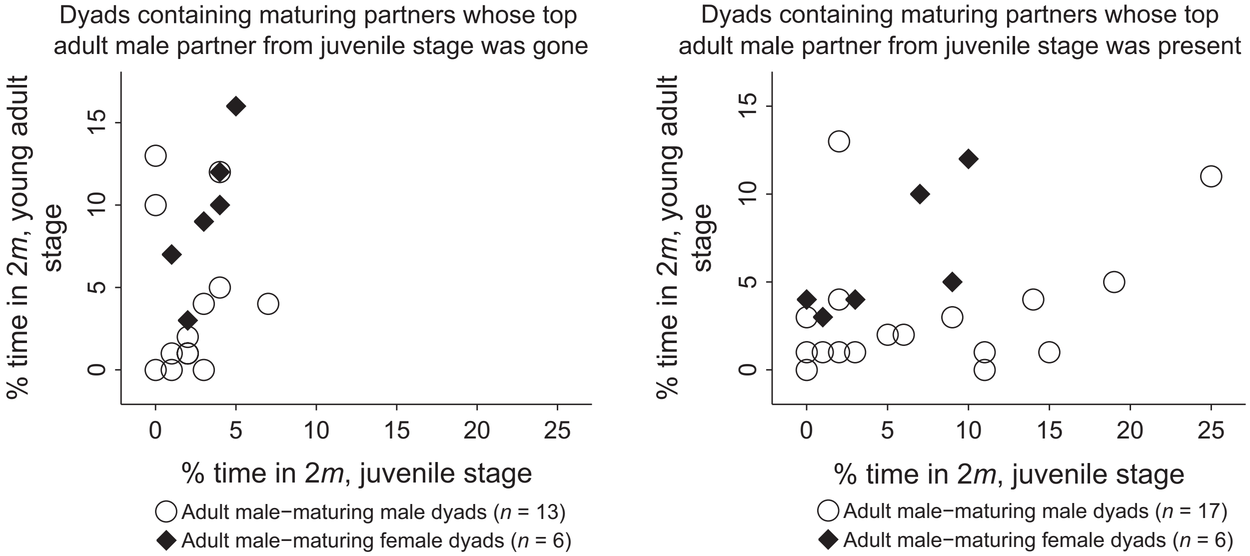

Fig. 3: Visually, young adult animals that lost their top adult male proximity partner from the juvenile stage appeared to develop strong new proximity relationships with other adult males, rather than forgoing time near adult male partners. For maturing animals that still had their top proximity partner from the juvenile stage available, juvenile stage proximity relationships appeared to predict young adult stage preferences.

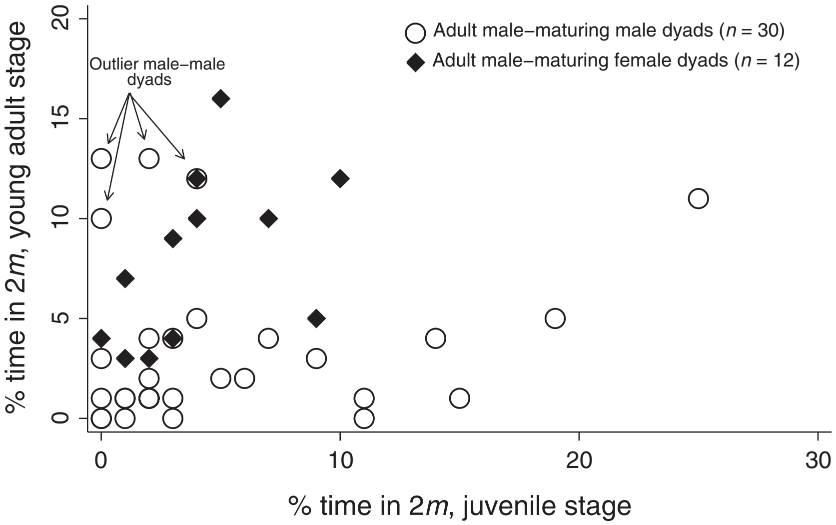

Fig. 4: Juvenile stage proximity relationships predicted young adult stage proximity relationships for adult male–young adult female dyads better than for adult male–young adult male dyads. The result was highly influenced by four outlier male–male dyads. Three of these young adult males had lost their top adult male proximity partner from the juvenile stage; the fourth now spent equal time with his previous top adult male partner, and his social group's new dominant male. For females, juvenile stage proximity relationships were highly predictive of young adult stage proximity relationships even if they had lost the adult male partner they originally spent the most time with. Their juvenile stage proximity relationships predicted which males they would 'switch' to.

adult males with whom they had previously spent very little time.

For males, however, the pattern was different. Young males whose top juvenile proximity partner was no longer present formed close ties to adult males with whom they had previously spent very little time. Four notable outliers spent much more time in close proximity to an adult male in the young adult stage than their time with that male in the juvenile stage might predict (Fig. 4; simple slope = 0.128). Three of these young adult males had lost their top juvenile proximity partner, but one had not. All four dyads contained former subordinate adult males who were now alpha (three adult males) or beta (one adult male) rank. These outlier dyads meant there was no clear relationship between male–male dyads' proximity patterns at the juvenile and young adult stages.

To evaluate this more systematically, we tested three models. The first model (Table 3a) contained the four main effects predictors. The results showed that adult male–maturing female dyads spent more time in close proximity in the young adult stage than adult male–maturing male dyads did, and that proximity relationships during the juvenile stage were only weakly predictive of young adult stage proximity relationships ($p = 0.098$). Adult male rank and the presence/absence of top juvenile proximity partners did not predict proximity relationships.

In the second model (Table 3b) we dropped the presence/absence of top juvenile proximity partner variable because it was not predictive, and replaced it with the interaction term for sex and juvenile proximity relationships. In this model, the proximity relationships of adult male–young adult female dyads were predicted by juvenile stage proximity relationships, but the same was not true for adult male–maturing male dyads. This model provided a better fit to the data (i.e., had a lower AICc, with an ΔAICc of 6.01) than the model containing only the four main effects. In the third model (Table 3c), we retained the interaction term, but excluded the four outlier dyads discussed above (Fig. 4). Without these dyads, proximity relationships in the juvenile stage predicted proximity relationships in the young adult stage for both sexes.

Do Proximity Patterns Suggest Father/Daughter Inbreeding Avoidance?

We found no evidence that genetic paternity influenced changes in adult male–maturing female proximity relationships across time. All four father–daughter dyads spent more time together when the female was a young adult than when she was juvenile (mean change = 4.3%, SD = 2.1%). For the eight unrelated dyads, seven spent more time together when the female was a young adult than when she was a juvenile, and one spent less time together (mean change = 3.6%, SD = 4.7%). After controlling for male rank, paternity had no effect on dyads' change in time spent in close proximity (β = 0.017, SE = 0.020, z = 0.89, p = 0.376, n = 12).

Discussion

Our data replicate results from previous studies which found that young gorillas have stronger proximity relationships with higher ranking males than lower ranking males (Fossey 1979; Stewart 2001; Rosenbaum et al. 2011). They also extend previous findings to demonstrate that growing animals maintain these relationships as they mature into subadults and young adults. We predicted that adult male–maturing male dyads would have more stable proximity relationships across time than adult male–maturing female dyads. This prediction was partially supported by the data. While juvenile stage relationships predicted subadult stage relationships for both sexes, the effect was stronger for male-male dyads than for male-female. For maturing females, who may reproduce in their natal groups or disperse to other social groups, it may be advantageous to develop relationships with a range of males before making life-history decisions with important fitness consequences. However, once maturing animals were young adults, male–female proximity relationships were remarkably strong, and very well predicted by with juvenile stage proximity relationships. Male–male relationships at this stage waned in strength, although juvenile stage proximity relationships predicted young adult stage relationships for most dyads.

These data raise two related questions. First, why do maturing gorillas have the strongest relationships with high-ranking adult males? Second, what benefits do gorillas gain from sustaining these relationships across time?

Why Dominant Males?

Young animals may spend the most time near high-ranking males because these males provide the most effective protection against infanticide, an important source of infant mortality (Watts 1989; Robbins et al. 2013). As in many other species, male dominance rank in gorillas is correlated with reproductive success (Bradley et al. 2005; reviewed in Ellis 1995). Thus, paternity may favor strong ties between high-ranking adult males and infants. In addition, in species like gorillas with intense competition for access to females, dominance rank is expected to be associated with phenotypic quality (e.g., Clutton-Brock & Harvey 1976; Andersson 1994; Fischer et al. 2004). It may be less costly for high-quality males to protect infants than for low-quality males to do so. This could increase the likelihood that they will provide protection for infants even in the absence of high degrees of paternity certainty.

We speculated that male rank might hold less predictive power for adult male–maturing animal relationships once the maturing partner no longer required much protection. The data supported this speculation. While rank was still a statistically significant predictor of proximity relationship strength in the subadult stage, the size of the effect was half that of the rank predictor in the equivalent juvenile stage model. By the time maturing animals were young adults, male rank no longer predicted their proximity relationships. This is further evidence that one of the primary functions of relationships between adult male and infant gorillas is protection.

Why Maintain Early Relationships?

Explanations for long-term social relationships typically fall in one of two categories: in specific ecological conditions, long-term relationships enhance survival and reproductive success regardless of relatedness (e.g., baboons: Barton et al. 1996; dolphins: Lusseau et al. 2003); or animals gain inclusive fitness benefits when they form long-term relationships (e.g., female and some male lions, Packer et al. 1991; black-tailed prairie dogs: Hoogland 2013). Mountain gorillas live in a particularly favorable environment in which differential access to food appears to have little effect on dispersal decisions or female reproductive success (e.g., Robbins et al. 2007, 2009b). Therefore, it seems unlikely that ecological conditions provide a good explanation for sustained proximity relationships. It is more likely that long-term relationships between infants and adult males begin as a form of parental care or investment, and function to protect young animals from infanticide. However, as infants mature and become less vulnerable relationships between adult males and subadult or young adult animals may serve other purposes. The function of these long-term relationships may differ for maturing males and females.

Benefits for Maturing Males

Even though juvenile stage proximity relationships predicted young adult stage relationships for male–male dyads, relationship strength declined precipitously over time. This is unsurprising, as adult male mountain gorillas in heterosexual groups generally have weak social relationships with one another (Robbins 1996). Such relationships no longer serve a protective function, and the maturing animals in our sample were old enough to be viable reproductive competitors by the young adult stage (Vigilant et al. 2015).

Nonetheless, when the young adult males were spending time in close proximity to older males, their juvenile stage social relationships generally predicted which male it would be. For 26 of the 30 adult male–maturing male dyads, proximity relationships in juvenilehood predicted proximity relationships in young adulthood. This occurred despite probable fading quality of aging male partners. By 2011, two adult males who accounted for 12 adult male–maturing male dyads were 25 and 33 yr old, and both had younger males in their groups who were almost certainly better competitors (though note that the aging males still maintained alpha or beta dominance positions; KRC long-term records). Rather than proximity relationships changing to mirror these social dynamics, all young adult males save one (discussed below) continued to have the strongest proximity relationship with the adult male they had spent the most time near 7 yr earlier, provided that male was available to them.

Four young adult males in our sample developed strong new proximity relationships with adult males they had spent either no or very little time near to as juveniles. Three of them had lost their top adult male partner from the juvenile stage. The disappearance of a maturing animal's top adult male partner from juvenilehood would not necessarily have to result in 'replacement' as they are far past needing protection. Instead of forgoing time near adult male social partners, these animals instead developed remarkably strong new proximity relationships with adult males they spent little or no time near when they were juveniles. One dyad developed a strong new proximity relationship despite the continued presence of the maturing partner's top adult male social partner from the juvenile stage, but this was an isolated case. However, the new proximity relationship did not appear to replace the old one; the maturing partner had equally strong proximity relationships with both adult males.

All four of the adult males in these dyads were animals who had risen sharply in rank over the course of the study. One had been a 3rd ranked male in 2004 and was the dominant male in his group in 2011. Two others were subordinate males in 2004, but were the dominant males in their groups in 2011. The last was a subordinate male in 2004 and 2nd ranking in 2011. These adult males would not have been particularly valuable social partners when the maturing males were juveniles. After they became high ranking, their value probably increased. These four relationships are particularly interesting because as stated above, in general relationships among this demographic are weak (Robbins 1996). Perhaps maturing males whose earlier proximity relationships predicted later relationships could depend on tolerance from their long-time older male partners, while those who were developing new relationships could not and so worked harder to cultivate or maintain such relationships.

Even if relationship strength attenuates, maintaining relationships with older adult males may have multiple advantages for maturing males. It provides closer proximity to adult females, who tend to congregate around the top-ranked male(s) (e.g., Harcourt 1979; pers. obs., but see also Stoinski et al. 2009a). Even if maturing males do not regularly obtain mating opportunities until they are fully grown, it may occasionally pay off sooner; in this population, males as young as eight have sired infants (Rosenbaum et al. 2015; Vigilant et al. 2015). For most males, however, such proximity could assist in later mating efforts. It may also help maturing males diminish the likelihood of aggression from older competitors as they become big enough to be serious rivals. Finally, it might help young males gain a better place in the queue for reproductive access behind older, higher ranking animals (Robbins & Robbins 2005).

Benefits for Maturing Females

While male–male dyad relationship strength declined sharply between the juvenile and young adult developmental stages, no such drop occurred for the male–female dyads. Eleven of 12 adult male–maturing female dyads that were coresident in the young adult stage spent more time in close proximity when the female was a young adult than they did when she was a juvenile. Juvenile females' proximity relationships strongly predicted their proximity relationships when they became young adults. This is particularly striking because half of the young adult females in our sample resided with males who had experienced substantial rank changes or moved into newly formed groups after fissions. Females' relationships with older males are unlikely to directly increase their reproductive output since female gorillas, like most mammals, are not limited by access to male reproductive partners. However, a female's choice of male social partner is important as males help ensure infant survival, and reproductive age females continued to rely on long-term adult male social partners. It is not clear why young adult females continued to associate closely with the same adult males that they had associated most with when they were juveniles despite possible fading quality. Robbins (2001) found that social behavior patterns during the 3 yr preceding a group split predicted which adult male adult females chose to join (but see also Watts 2003). The current data suggest that relationships can go back much further and extend beyond favorable breeding partners. Perhaps the acquired data females have on the reliability of a long-term adult male social partner outweighs the potential risks of associating with an aging male. More work is needed to determine whether such dyads reproduce together, or whether lifelong relationships suppress mating behavior as is the case for many other primate species (e.g., Paul & Kuester 2004; Muniz et al. 2006).

Benefits for Adult Males

Previous work on this population indicated that high-ranking males may offer younger/subordinate males breeding concessions to retain them as group members (Stoinski et al. 2009b). This may be beneficial to high-ranking males because multimale groups have lower rates of infant mortality (Robbins 1995; Robbins et al. 2009b) and female emigration (Robbins et al. 2009a; but again see Robbins et al. 2013 for the most recent data). Dispersing males may also have lower lifetime fitness than philopatric males (Robbins & Robbins 2005). Therefore, the inclusive fitness benefits of giving younger males (particularly sons) breeding opportunities, plus improved infant survival and female retention, may offset older males' lost breeding opportunities. It is yet to be determined whether, and how, relationships between adult males and maturing males influence dispersal decisions and reproductive opportunities for maturing males.

Adult males might benefit from maintaining relationships with maturing females as well. Female preference is an important component of male mating success in mountain gorillas (Fossey 1982; Watts 1991; Harcourt & Stewart 2007). Having female 'friends' may help males maintain or elevate their dominance rank, even if these dyads do not reproduce. The presence of such females may encourage young males to remain in the group, and this in turn can help groups to retain additional females (Robbins et al. 2013). Relationships between fathers and adult daughters could also allow males to protect their grandchildren from infanticide and predation.

Conclusions

These data add to our understanding of the socioecology of species with a slow life history in two important ways. First, enduring relationships between maturing gorillas and adult males, who may be their fathers but are unlikely to be females' mates, suggest that kin selection may shape male–female and male–male relationships in this species to a greater extent than previously suspected. The fact that maternal absence predicts adult male dispersal in this population (Stoinski et al. 2009a) suggests that mother–son relationships remain important for males even after they reach adulthood. Our data suggest that father–daughter relationships may have a similar impact. This is striking because there are very few non-human primate species in which adult offspring reside in groups with their opposite sex parents. Exceptions include the cooperatively breeding *Callitrichids* in which offspring typically do not reproduce (French 1997), white-faced capuchin monkeys (Muniz et al. 2006), and chimpanzees and bonobos, where adult males may live in the same groups as their mothers (e.g., Boesch 2009; Surbeck et al. 2011). Sexually mature offspring living with opposite sex parents raises the potential for inbreeding, but may also provide opportunities for cooperation, support, and protection.

Second, our data indicate that young adult males generally maintain enduring proximity relationships with the same males that they associated with when they were younger. However, if their primary partners die or leave the group, they are able to form strong relationships with newly dominant males. This suggests that males may be sensitive to political forces, like male chimpanzees (e.g., de Waal 1982, 1984; Nishida & Hosaka 1996; Mitani et al. 2000; Duffy et al. 2007), but there is no evidence that male gorillas routinely facultatively shift social allegiances in response to changing group dynamics. More work is needed to determine whether young males gain lifetime fitness advantages from associating with high-ranking males, and whether such relationships are cultivated by young adult males or their older male partners.

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