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Who's your daddy? The causes and consequences of male-immature relationships in wild mountain gorillas (Gorilla beringei beringei)

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Who's your daddy? The causes and consequences of male-immature relationships in wild mountain gorillas (*Gorilla beringei beringei*)

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Doctor of Philosophy in Anthropology

By

Stacy Lynn Rosenbaum

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ABSTRACT OF THE DISSERTATION

Who’s your daddy? The causes and consequences of male-immature relationships in the mountain gorilla (*Gorilla beringei beringei*)

By

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Doctor of Philosophy in Anthropology
University of California, Los Angeles, 2014
Professor Joan B Silk, Chair

Among mammals, humans are unusual for their bi-parental care. Expensive gametes, gestation, and lactation necessitate the Phylum-typical extensive female investment, but in all cultures across the globe men take part in caring for children. The form, duration, and extent of their care varies, but it is nonetheless a human universal. Across the primate order, about 40% of species provide male care of immatures in some form. The majority of studies of male parenting in our closest extant relatives have taken place in a few small-bodied, monogamous or polyandrous species of New World monkeys, the Callithricids. While highly informative, the social structure and ecology of these species bears little resemblance to that of modern-day humans or the hominins who shared our recent evolutionary past. By studying male-immature relationships in primates that are more closely related to us and that live in social systems closer to “species-typical” (i.e. highly flexible) for *Homo sapiens*, we can get a clearer picture of the evolution of male care and investment in offspring.

The mountain gorilla (*Gorilla beringei beringei*) is an excellent model for examining the form and function of such relationships in a close human relative. The genus *Gorilla* split from the genus *Homo* ~10 million years ago. Although not our closest living relative, *Gorilla beringei* is one of the few primates species besides humans in which both males and females can either reproduce in their natal group or disperse. For years they were described as strictly polygnous with one male and multiple females in each group, but after 47 years of research we now know that they are also capable of remarkabe flexibility in their social system. About 40% of the the gorillas monitored by the Dian Fossey Gorilla Fund’s Karisoke Research Center in the Virunga Massif in central Africa occur in multi-male, multi-female groups.

In mountain gorilla groups, male-immature relationships are conspicuous for their closeness. Males are highly tolerant of young animals, and immatures often cluster around adult males as soon as they are old enough to be independently mobile. Besides their mother, an adult male (usually but not always the dominant animal) is typically an immature’s closest adult social partner. Adult males are key to infant survival, protecting them from infanticidal outsiders, and probably historically, predators as well.

In this dissertation, I examine 1) whether males and immatures are capable of discriminating paternity in multi-male, multi-female groups; 2) if, and how, mother gorillas facilitate relationship development between their infants and a protective adult male(s); and 3) whether social preferences early in an immature’s life for certain adult males predict their social preferences at two later developmental stages, including young adulthood. Together, these chapters give us a more nuanced understanding of male parenting behavior and its evolutionary implications in one of our closest living relatives, *Gorilla beringei*.

The dissertation of Stacy Lynn Rosenbaum is approved.

Daniel T Blumstein
Susan B Perry
Brooke A Scelza
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2014

This work is dedicated to the men and women who have given their lives while protecting Africa’s wildlife. We are forever in your debt.

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Biographical Sketch

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2010	MA, Anthropology (University of California-Los Angeles)
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2014	National Science Foundation Behavioral Endocrinology Postdoctoral Fellow (Lincoln Park Zoo, Chicago Illinois)
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Peer-reviewed publications

Rosenbaum S, Silk JB, & Stoinski TS (2011) Male-immature relationships in multi-male groups of mountain gorillas (*Gorilla beringei beringei*). *American Journal of Primatology*, 71, 1-10.

Stoinski TS, Rosenbaum S, Ngaboyamahina T, Vecellio V, Ndagijimana F, & Fawcett K (2009) Patterns of male reproductive behavior in multi-male groups of mountain gorillas: examining theories of reproductive skew. *Behaviour* 146(9), 1193-1215.

Stoinski TS, Vecellio V, Ngaboyamahina T, Ndagijimana F, Rosenbaum S, & Fawcett K (2009) Proximate factors influencing dispersal decisions in male mountain gorillas. *Animal Behavior* 77(5), 1155-1164.

Conference presentations (selected)

Rosenbaum S, Hirwa JP, Silk JB, & Stoinski TS (2014) The effects of paternity certainty and infanticide risk on maternal behavior toward silverback mountain gorillas (*Gorilla beringei beringei*). *XXV Congress of the International Primatological Society*. Hanoi, Vietnam: Abstract #935.

Rosenbaum S (2014) The development of male social partner preference in maturing mountain gorillas (Gorilla beringei beringei). *8th Annual California Workshop on Evolutionary Social Sciences*. San Luis Obispo, CA.

Rosenbaum S, Hirwa JP, Silk JB, & Stoinski TS (2012) Long-term social partner preferences between adult male and maturing mountain gorillas (*Gorilla beringei beringei*). *XXIV Congress of the International Primatological Society.* Cancun, Mexico: Abstract #258.

Hirwa JP, Stoinski TS, & Rosenbaum S (2012) Ontogeny of sibling relationships in the mountain gorilla: does inclusive fitness influence sibling interactions? *XXIV Congress of the International Primatological Society.* Cancun, Mexico: Abstract #246.

Rosenbaum S & Stoinski TS (2009) Variance in male/immature relationships in the mountain gorilla. *American Journal of Primatology* 71 (Suppl 1), 96.

Invited talks (selected)

2014	The development of male social partner preferences in maturing mountain gorillas (Center for Behavior, Evolution, and Culture, University of California-Los Angeles, CA)
2014	Male-immature relationships in the mountain gorilla, a socially flexible primate species (Primate Research Institute, Kyoto University, Japan)
2014	Maternal facilitation of male/infant relationships in the mountain gorilla, *Gorilla beringei beringei* (Wildlife Research Center, Kyoto University, Japan)
2013	Biological anthropology: an introduction to the comparative approach (Baruch College, New York NY)
2012	Using research to conserve Rwanda's mountain gorillas (University of Wisconsin-Madison Arboretum, Madison WI)
2012	Integrating research and conservation: Rwanda's mountain gorillas as a case study (Lincoln Park Zoo, Chicago IL)

Teaching & mentoring

2014	Instructor: Introduction to Human Evolution (UCLA)
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2008-2013	Course reader: Models of Cultural Evolution; Human Behavioral Ecology; Primate Behavior Non-Human to Human; Great Adaptations: Origins of Complexity in Nature; Survey of Biological Evolution; Evolution & Human Sexuality (UCLA)

Chapter 1

Human parenting in an evolutionary context

Extremes, be they behavioral, morphological, or physiological, require explanation. Such phenomena challenge our scientific theories and expand our understanding of the evolutionary pressures underlying present-day variation. *Homo sapiens* are the only extant primate species whose mating systems include monogamy, polygyny, polyandry, and promiscuity (Mealey 2000). This diversity carries tremendous implications for child rearing in a species that heavily invests in its offspring. Human parental investment is unique in the animal kingdom for its combination of extended duration and intensity. Children are extremely costly (Altmann 1987, Lancaster & Lancaster 1987, Knott 2001, Robson et al. 2006, Hrdy 2009), and in many cultures are raised by not only by both parents, but a small army of helpers that include siblings, grandparents, aunts and uncles, and even friends. Our expensive babies rely on parental effort through an extended childhood and often well beyond, and in spite of this, we have the shortest inter-birth interval of any living great ape. No other animal on earth invests as heavily in its offspring as human parents.

The role of fathers in parenting is highly variable across cultures (Marlowe 2000, Hewlett 2000, Lamb 2000; but see Hawkes 1991). While fathers in all cultures are involved with their children in some way (e.g. financial contributions, protection, direct care, social support etc.), the type, extent, and duration of involvement is diverse. The importance of male contributions to offspring growth and development has perhaps been underestimated historically. Traditional anthropological studies typically only measured direct supportive behavior when children were young, such as providing food (e.g. Marlowe 1999, Hames 1992) or playing with/holding them (e.g. Hewlett 1991, Flinn 1992, Marlowe 1999, Tronick et al. 1987), and males tend to engage in less of these behaviors than female caretakers. However, other work has demonstrated that fathers may play a crucial role during discrete windows, making their contributions harder to detect than the obvious direct care mothers provide (e.g. Scelza 2010, Marlowe 2003, King 1994, Flinn 1988).

The remarkable diversity of paternal contributions to offspring survival and growth raise questions about the evolutionary origins of such behavior. Human males in all mating systems across all cultures parent, despite evolutinary pressure that may frequently make their efforts appear maladaptive (see below). In this dissertation, I investigate male parenting behavior in a socially flexible great ape, the mountain gorilla (*Gorilla beringei beringei*). Most studies of male parenting in non-human primates have occurred in a few species of small-bodied, socially monogamous or polyandrous species. While informative, these studies alone fail to capture the variation in mating systems and parenting behaviors that occur across the Primate order. Our very recent evolutionary split from the genus *Gorilla,* plus their remarkable ability to live in a wide range of social configurations, make them an excellent model species to investigate the evolutionary origins of male parenting in *Homo sapiens*.

Male parenting in mammals: impediments and alternative functions

Mammalian mothers are locked into a significant investment with the conception of each fetus. Females produce expensive gametes, and obligatory gestation and lactation require considerable time and energy. These physiological limitations create a strict upper bound on the number of offspring a female can produce in her lifetime. No amount of calories, helpers at the nest, or protection from predation can push a female's fitness past the time limits set by gestating and lactating. These constraints mean that offspring loss is costly; by the time infants are born, females have already invested a considerable amount. Males, on the other hand, can produce a nearly unlimited supply of inexpensive gametes and have no obligatory investment in most species beyond providing sperm during conception. Their fitness limitations are dictated by the number of proceptive females they can find and impregnante than by time or direct energetic costs (Trivers 1972).

These physiological realities create different cost/benefit ratios of parental investment for males and females. Females can increase their reproductive success by securing access to calories and/or protection that ensure offspring they have already conceived can grow and survive. When compared to females, males have more to gain from seeking additional mates than from caring for existing offspring. Males who "stay at home" to help raise a small number of offspring are, in general, outcompeted by males who terminate investment after conception to search for additional mates (Trivers 1972). It is hardly surprising, then, that across the Mammalian class male parenting is rare. Males care for their offspring in less than 10% of species (Kleiman and Malcolm 1981).

Males have a second impediment to parenting not unique to mammals. Females enjoy 100% confidence the offspring they are investing in are their own, but few males have the same assurance. This further dilutes the benefits of parenting for males. Those that do almost invariably have mating systems that mitigate (but not eliminate) paternity uncertainty (Alexander et al. 1979, van en Berghe 1979, Bales 1980, Snowdon & Suomi 1982, Kurland & Gaulin 1984, Smuts & Gubernick 1992), or exploit ecological niches where male care dramatically improves offspring surivival rates (e.g. bamboo rats: Silva et al. 2008; Tengmalm's owl: Korpimäki et al. 2011; Clutton-Brock 1991). However, advances in non-invasive molecular genetics have demonstrated that extrapair paternity rates can be remkarably high even in socially monogamous species (e.g. Ethiopian wolves 28% (Randall et al. 2007); fat-tailed dwarf lemurs 44% (Fietz et al. 2000); rock wallaby 33% (Spencer et al. 1998); reviewed in Cohas & Allainé 2009). Since investing in offspring that might belong to another male is costly, it is unsurpsing that few male mammals provide parental care.

While males provide some form of parental care in <10% of mammal species, rates are not distributed equally across orders; male care occurs at much higher rates in primates than in most other orders. In approximately 40% of primate species, males provide some kind of care. They play varied roles in the lives of immatures, ranging from extensive paternal care in callitrichids and humans (e.g. Santos et al. 1997, McGrew 1988, Tardif et al. 1990, Geary & Flinn 2001) to minimal contact in many taxa (e.g. orangutans: van Schaik & van Hooff 1996; lemurs: Hilgartner et al. 2006, Wright 1990; see Whitten 1987 for an overview). Unsurprisingly, species that typically live in multi-male groups where females regularly mate promiscuously almost invariably demonstrate less male care. Nevertheless, adult male involvement with infants is regularly reported in multi-male groups of primates, especially Old World monkeys and great apes.

Male care of immatures does not necessarily have to be parenting effort. Alternative explanations include mating effort and future alliance building. In species where dominance rank is highly correlated with reproductive success, subordinate males may use infant care as an alternative mating tactic. Building relationships with infants may increase their chances of future matings with an infant's mother (Smuts 1985, Gross 1996). If male dominance rank tenures are long, males may use early relationships with immatures to build support for future alliances (Strier 1993). While we know that these alternative functions apply to some males of some species, many male/immature interactions are best explained as possible parenting effort, even in multi-male social groups where paternity certainty is low.

If males in multi-male groups are indeed parenting, the benefits males might derive depend on their ability to discriminate between their own offspring and those of other males. For many years, it was assumed that primates could not identify paternal kin (see Rendall 2004 for a review), but a growing body of evidence indicates this assumption may not always be true. Male baboons selectively support their own offspring in agonistic encounters (Buchan et al. 2003), and fathers and infants associate more than unrelated male-infant dyads (Huchard et al. 2012). Male chimpanzees direct less aggression toward, and play more with, their own offspring than with unrelated infants (Lehmann et al. 2006). Hanuman langurs protect only infants of which they are potential sires against infanticidal males in multi-male groups (Borries et al. 1999). Male rhesus macaques interact more with their own offspring than with unrelated immatures (Langos et al. 2013). There is considerable uncertainty about the mechanisms that underlie paternal kin recognition, but these may include age difference, familiarity mediated through the mother's association with former mates, or phenotypic matching.

Why mountain gorillas? Justification of the model species

Mountain gorillas (*Gorilla beringei*) live in both multi and single-male groups, making them a particularly valuable model for examining the form, mechanisms, and function of male-immature relationships. Male-immature relationships are a conspicuous feature in gorilla societies. Immature animals are attracted to adult males from a young age, and most males are remarkably tolerant of immatures (Stewart 2001, Yamagiwa 1983, Fossey 1979). Young gorillas associate with and groom adult males, and adult males provide protection against infanticide and predation (Harcourt & Stewart 2007, Watts 1989, Robbins et al. 2013). Despite these strong relationships, few detailed studies of male-immature relationships in gorillas exist; Dian Fossey discusses such relationships briefly in her writing, but the only systematic study before this dissertation work was conducted at the Karisoke Research Center in the 1970's by Dr. Kelly Stewart (Stewart 2001).

Since Stewart's original study, the mountain gorilla groups monitored by the Dian Fossey Gorilla Fund International at the Karisoke Research Center have become larger and increasingly multi-male. Average group size has increased from 12 to 18 individuals per group (Stoinski et al. 2009), and the male to female ratio has shifted from 1:2.4 to 1:1.5 (Karisoke long term records). Population wide, 40% of groups contain more than one adult male (range 2-9, Gray et al. 2010). The shifting demographics of the Karisoke gorilla groups may have affected social dynamics between males, mothers, and their offspring. In multi-male groups, alpha males dominate mating opportunities, but lower-ranking males sire some offspring (Stoinski et al. 2009, Bradley et al. 2005). This likely creates more paternity uncertainty. In addition, immatures now have a wider variety of potential male partners. Reduced paternity certainty and the presence of alternative partners may systematically alter the dynamics of male-immature relationships.

The genus *Gorilla* possesses extreme morphalogical characteristics typical of a species that evolved to live in one-male, multi-female groups. They are among the most sexually dimorphic of all primate species, and males have well-developed weaponry, small testes, and slow-swimming sperm (Crook 1972, Leutenegger & Kelly 1977, Harcourt et al. 1981, Møller 1988). Although bi-male groups have been reported since the 1950's when George Schaller first conducted long-term study of the species (Schaller 1963), groups containing multiple fully adult males (some related, some unrelated) observed from the late 1990's through the 2000's may well be an evolutionarily novel social group configuration for this species. However, there is evidence that multi-male groups have fitness advantages for both males and females, which raises questions about how long this configuration has existed, and whether it is an evolutionarily stable strategy.

In the following chapters, I will examine 1) whether male gorillas and the immatures in their groups discriminate paternity; 2) if, and how, females of young infants modify their behavior to facilitate relationship development between their infant and a protective adult male, and 3) whether social preferences between males and immatures persist as immatures mature through subsequent developmental stages. Together, these chapters give us a more nuanced understanding of male parenting behavior and its evolutionary implications in one of our closest living relatives, *Gorilla beringei*.

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Chapter 2

The effects of paternity and male rank on male-immature relationships in the mountain gorilla (*Gorilla beringei beringei*)

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Abstract

Kin discrimination mechanisms are expected to evolve when they provide fitness benefits. To date, the evidence for kin discrimination is mixed across taxa and mating systems even when it would be apparently beneficial. In animals with promiscuous mating systems, males were long believed to abstain from parenting behaviors partly because the costs of potential offspring misidentification outweighed the benefits of dual parenting. Conversely, males in monogamous systems could parent because of their high paternity certainty. However, recent work has shown that in some species males parent despite high rates of false paternity, and that males in some promiscuous systems discriminate between their own and other males' offspring. Adult male mountain gorillas (*Gorilla beringei beringei*) and the immature animals in their groups have close relationships even when paternity certainty is low, and these relationships are best explained as low-cost parenting behavior. Using an information theoretic approach, here we evaluate the impact of male rank, paternity, and age difference on male/immature relationships in wild multi-male gorilla groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center. In our sample of 21 adult males and 50 genotyped immatures, males and 1-5 year old immatures clearly use male rank, not paternity or age difference, to choose preferred social partners. Male/immature dyads were closer social partners in 2011-12 when reproductive skew was low and group size smaller, than comparable dyads in 2003-04 when skew was high and group size larger. Gorillas' lack of paternal kin discrimination provides further behavioral evidence that the species' multi-male social structure is evolutionarily novel. However, patterning of male-immature relationships and genetic paternity suggest a persistent minority of bi-male groups throughout *Gorilla beringei's* evolutionary history. This may help explain their ability to live for extended periods in multi-male, multi-female social units despite possessing morphological characteristics typical of harem systems.

Introduction

Kin discrimination is useful whenever social structure facilitates cooperative behavior (Hamilton 1964) or enables deleterious inbreeding (Lehmann & Perrin 2003, Blouin & Blouin 1988). Selection pressure should favor kin discrimination in systems where 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: Tardif et al. 1990, Mendoza & Mason 1986, Achenbach & Snowdon 2002; rodents: Wynne-Edwards 1987, Cantoni & Brown 1997, Jones & Wynne-Edwards 2000, Silva et al. 2008; birds: Webster et al. 2007, Wan et al. 2013, reviewed in Cockburn 2006; fish: DeWoody et al. 2000, Balshine-Earn & Earn 1997, Itzkwitz et al. 2001) or species that rely heavily on cooperative behavior for mating access, offspring rearing, territory control, or food acquisition (e.g. social insects: reviewed in Beshers & Fewell 2001; Old World primates: Mitani et al. 2000, Muller & Mitani 2005, reviewed in Silk 2002; social carnivores: Villiers et al. 2003, Packer & Pusey 1982, Mosser & Packer 2009; communal rearers such as eiders (Öst et al. 2003 & 2008) or house mice (Weidt et al. 2008, König 1994)). Although such species are unusual, selection pressure for kin discrimination should also be strong in organisms that reach sexual maturity while living with close kin of the opposite sex (e.g. capuchins: Muniz et al. 2006; northern muruquis: Strier et al. 2011; mountain gorillas: Stoinski et al. 2009a, Robbins et al. 2009).

To date there is mixed evidence for kin discrimination across such taxa and mating systems. Most bird species are socially monogamous and provide biparental care, but ~11% of offspring are a result of extra-pair paternity (Griffith et al. 2002) and males appear unable to detect it (Kempenaers & Sheldon 1996). Pair-bonded fat-tailed dwarf lemurs have extraordinarily high rates of extra-pair paternity (44%), yet males do not reduce care accordingly (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 et al. 2000; honey bees: Châline et al. 2005; ants: Holzer et al. 2006, Friend & Bourke 2012).

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 cooperate/associate preferentially with kin. This includes some insects (e.g. Lizé et al. 2006, Lihoreau & Rivault 2009); social carnivores (e.g. Wahaj et al. 2004, Leclaire et al. 2013) and many primates (e.g. Wikberg et al.

2013, Albers & Widding 2013, Langos et al. 2013, Charpentier et al. 2007, Huchard et al. 2012, Eberle & Kappeler 2006; 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 strong, reliable cues to maternal identification. For fathers, the task is more difficult. In species that form pair bonds or one-male groups, males may use proxies like co-residence to detect offspring, but the reliability of these proxies vary across species. For example, the high rates of extra-pair 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 multi-male 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. But, advances in non-invasive 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 non-monogamous chimpanzees (Lehmann et al. 2006), baboons (Buchan et al. 2003, Huchard et al. 2012), mandrills (Charpentier et al. 2008), capuchins (Muniz et al. 2006), rhesus macaques (Langos et al. 2013), and langurs (Borries et al. 1999). The domains in which paternal kin discrimination appears include affiliative behavior, mate choice, and protection against infanticide.

Mountain gorillas (*Gorilla beringei beringei*) are unusual among primates because they regularly form both one-male and multi-male groups. About 40% of the gorilla groups in central Africa's Virunga massif are multi-male (Gray et al. 2010). Large numbers of adult males (range: 2-9) have (mostly) peacefully co-resided for years in mixed-sex groups, with remarkably low male- to-female ratios (Stoinski et al. 2009b). It is unclear whether there would have been evolutionary pressure for paternal kin discrimination to develop in mountain gorillas. This likely depends on how common multi-male 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, well-developed weaponry, small testicles relative to body size, and slow-swimming sperm

(Crook 1972, Leutenegger & Kelly 1977, Harcourt et al. 1981, Møller 1988). If one-male groups were historically the norm, then paternity certainty would likely have been high enough to preclude the need for any sophisticated recognition mechanism beyond co-residence. Extra-group mating has never been reported, and there are few known instances of females successfully raising offspring in groups where they were not conceived (Karisoke long-term records).

However, mountain gorillas are not only capable of living in multi-male groups, but may benefit from doing so. Advantages to living in multi-male groups include better female retention and lower risk of infanticide. Infanticide is 2-3 times more common in single-male groups than multi-male, and there is some evidence that females prefer multi-male groups (Robbins et al. 2013). 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 either disperse (for females, joining an established group; for males, starting a new group after a solitary period) or reproduce in their natal group (Harcourt et al. 1976, Watts 1991 & 2000, Robbins 1999, Robbins et al. 2009). Since females can reside with fathers through sexual maturity, females, and to a lesser extent fathers, should 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 defense. Previous studies hint that paternal kin discrimination may exist. Data from both Karisoke and Bwindi National Park, Uganda, suggest patrilineal relationships may be important during life history decisions like group fissions (Nsubuga et al. 2008) and dispersal (Harcourt & Stewart 1981). Furthermore, maturing gorillas have more stable social preferences for males who were of potential siring age when they were born, even if the male was not then dominant (Rosenbaum et al. in review).

Adult male and infant/juvenile mountain gorillas are exceptionally close social partners (Yamagiwa 1983, Stewart 2001). These relationships are best explained as low-cost paternal behavior (Rosenbaum et al. 2011), but previous analyses have not included 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 be lower than it was at the time Bradley and colleagues' data were collected. During the 2000s number of males per group increased and male-to-female ratio decreased, which corresponded with an increase in non-dominant males mating during windows of probable conception (Stoinski et al. 2009b) and lower reproductive skew (Vigilant et al. under review). About 25% of young animals spend more time with a non-dominant male than they do with the dominant individual (Rosenbaum et al. 2011), indicating there is variation in young gorillas' social preferences. Here we evaluate whether in multi-male mountain gorilla groups, male rank, paternity, male age at infant birth, or some combination of these variables best predict different facets of male-immature interactions.

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 2003-04 (508 hours), and the first and third authors in 2011-12 (1,019 hours), using 50-minutes focal follows of adult males (both time periods) and immatures (2011/12 only). The observers conducted regular inter-observer reliability tests in 2011-12. Proximity information was collected via instantaneous scan samples by the observers and extracted from the long-term Karisoke database. Fecal samples for non-invasive paternity analysis were collected by the observers and other Karisoke staff who were tested on individual identification of the animals. The total dataset includes 50 individual immatures and 21 individual adult males. The mean number of hours of focal data per dyad in 2003-04 was 25.9 (min=11.8, max=38.4), and the mean number of point scans was 229 (min=99, max=771). In 2011-12, the mean number of hours of focal data per dyad was 57.8 (min=14.5, max=99.8), and the mean number of point scans was 426 (min=100, max=795).

Dyad structure

The dyad is the unit of analysis. Each dyad is made up of an adult male ($\geq$ 12 years old), and an immature (1 - 5.9 years old (Watts & Pusey 1993); mean=3.4 years, SD=1.56 years). To be included in these analyses, the adult male partner must be at least 8 years older than the immature partner (mean=16.9 years, min=8.1, max=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 <12 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 et al. (2009b). Adult males are categorized as alpha (rank 1), beta (2), gamma (3). There are rarely enough displacements to determine exact ranks beyond 3rd, 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 2003-04 than in 2011-12 (Table 2.1; values are as of the midpoint of each data collection period). In 2003-04 we included every animal available in KRC's three multi-male research groups; in 2011-12, we included three of five multi-male groups. The other two were excluded because at the time of data collection the number of available immatures was ≤ 2.

Table 2.1

Study period	**# Grps**	**$\bar{x}$ Grp Size**	**$\bar{x}$ Males**	**$\bar{x}$ Immatures**
2003-2004	3	36 (range: 24-58)	6.33 (range: 6-7)	9.66 (range: 5-17)
2011-2012	3	23 (range: 12-42)	3 (range: 2-5)	5.66 (range: 4-9)

Table 2.1 Group composition in the two study periods

Behavioral measures

We evaluated 13 behavioral variables (Table 2.2). 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.

Table 2.2 Definitions of behavioral variables

Behavior	Definition	Directional?	Collection method*
Approach/leave interaction	One individual moves into or out of 2m range of another individual. Must remain within 2m for at least 5 sec	Yes	CFS
Time in close/ medium proximity	Within 2m/2-5m 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 sec	When initiator observed	CFS; D; ISS
Play	Non-aggressive interaction with both partners participating actively, engaging in behaviors such as hit, push, hold, wrestle, chase, play face, soft grunting etc.	No	CFS; D; AL
Co-feed (2011-12 only)	Two individuals feed within 1m of each other. Food source(s) of each individual must also be within 1m of feeding partner.	No	CFS; AL
Follow (2011-12 only)	Individual gets up and walks directly in the path of an individual leaving a resting or feeding space. Must be within 2m and 5 sec of the first animal leaving; must walk in direct path for at least 5m.	Yes	CFS
Carry	An adult male moves at least 2m transporting an infant ventrally or dorsally.	Yes	CFS; AL
Hold (2011-12 only)	An adult male picks up and holds an immature in his arms while sitting in one location.	Yes	CFS; AL
Carry	An adult male transports an immature at least 5m, either ventrally or dorsally.	Yes	CFS; AL
Vocal aggression	One individual pig grunts or screams at another.	Yes	CFS; AL
Non-contact aggression	One individual directs the following behavior(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

***ISS**=10 minute instantaneous scan samples; **CFS**=continuous focal animal sampling; **D**=duration collected; **AL**=ad libitum sampling

Highly correlated behaviors were combined to create composite indices for each dyad (see Silk et al. 2013). For each of the behavioral 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 dyadic index represent dyads that engaged in those behaviors 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 the rates of resting in physical contact and grooming ($\beta=3.21$, SE=0.32, z=9.90, $p<0.000$, n=203 dyads), and a second index based on rates of touching and social staring ($\beta=0.65$, SE=0.21, z=3.11, p=0.002, n=203 dyads).

Genetic paternity

We collected fecal 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 like allelic dropout. Sex was confirmed or determined using a PCR-based sexing assay (Bradley et al., 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 et al., 2007). Then, we conducted simulations that assumed either 5 or 9 potential sires and that 10% of potential sires were related at the half sibling level (R=0.25). The simulations assuming 5 and 9 potential sires were applied to datasets consisting of offspring with 6 or fewer potential sires and 7 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. As well as using CERVUS to assess the statistical confidence of our paternity assignments, we 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 in (Vigilant et al., in review; Rosenbaum et al. in prep).

Paternity was distributed among the males quite differently during the first data collection period and the second. In our 2003-04 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 and colleagues (2005). There was considerably less reproductive skew among the 2011-12 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%). Two males in the 2011-12 sample changed ranks between infant conception and when the behavioral data presented here were collected (one from gamma to beta, and the other from alpha to gamma). In the analyses reported below, we use the rank of the male when the behavioral data was collected. The mean age difference between fathers and offspring was 22.4 years in 2003-04 (min=9.6, max=28.1), and 16.0 years in 2011-12 (min=10.4, max=32.5). Fathers were significantly younger in the 2011-12 sample than in the 2003-04 sample (Mann-Whitney test: z=3.58, p<0.000) (Figure 2.1).

Figure 2.1

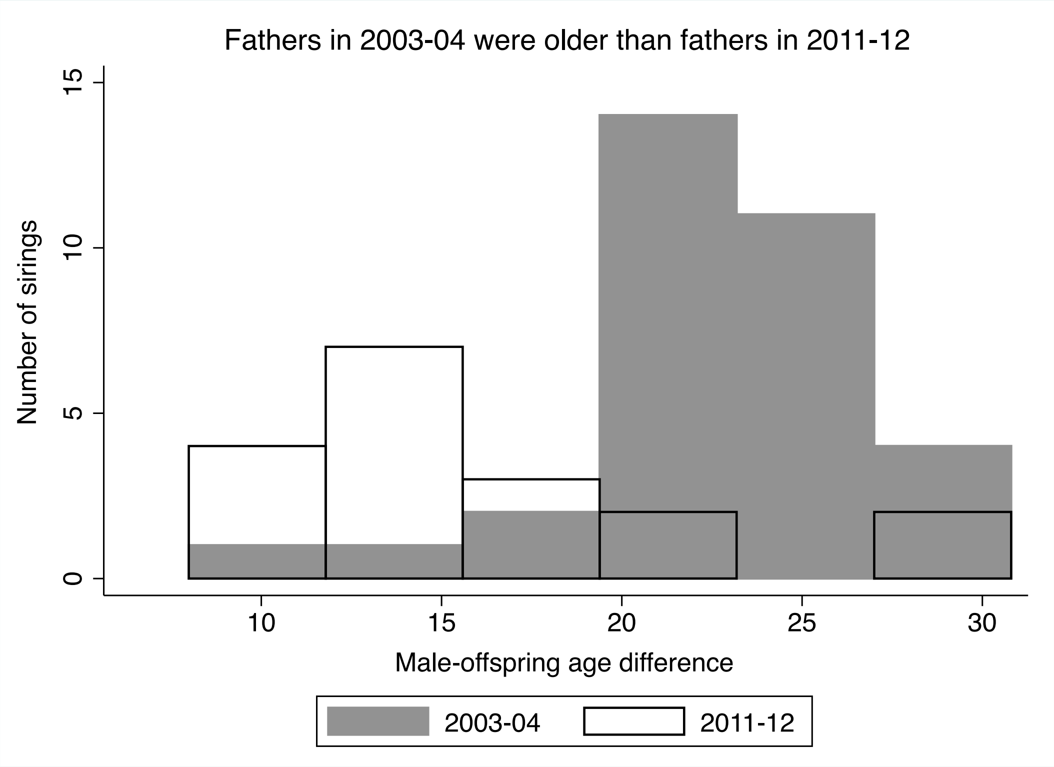

Figure 2.1 The mean age of genetic fathers in the 2011-12 sample was signficantly lower than in the 2003-04 sample.

There were five immatures living in groups without their father during the 2011-12 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 Karisoke. These five immatures were older than the rest of the sample (mean age of immatures with fathers present=3.25, SD=1.54, min=1, max=5.9, n=45; mean age of immatures without father present=4.72, SD=1.16, min=3.2, max=5.9, n=5; Mann-Whitney test:

z=1.96, p=0.050). These immatures were only included in analyses where they are explicitly compared to immatures who lived in their sire's group.

Data summary

Rates of behaviors 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. To determine who was primarily responsible for maintaining proximity, we calculated Hinde index values (Hinde & Atkinson 1970):

$$H=(IA/(IA+MA))-(IL/(IL+ML))$$

where MA= number of times the adult male partner approached the immature partner, IA= the number of times the immature partner, ML= number of times the male left the immature, and IL= number of times the immature partner left the male. This computes a proportion between -1 and 1; higher values indicate the immature was more responsible for proximity maintenance, and lower values indicate the 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 multi-level, mixed-effects regression models that treated individual animal IDs as a random effects parameter. *Ad libitum* data was used strictly as count data rather than calculating a rate. Visual examination of the data revealed possible differences in behavioral outcomes between the 2003-04 sample and 2011-12 sample. We used a dummy variable to evaluate study period effects, coded as 0 for the 2003-04 sample and 1 for the 2011-12 sample.

For each outcome variable, we evaluated fifteen 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 et al. 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 $\leq$ 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 model is the best fit out of all candidate models tested (Anderson & Burnham 2002, e.g. House et al. 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 with immatures. However, the quadratic term did not improve the fit of any models, and in most cases raised the AICc $\geq$ 5. Therefore, we also did not include 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 multi-level 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

Dyads spent more time in close proximity if the male partner was high ranking, and if they were in the 2011-12 study period. Two models had equal support: the model containing male rank and study period, and the model containing male rank only (Table 2.3). Weights suggest the model including both rank and study period is the most appropriate choice (Table 2.3). Visual inspection indicates the study period effect is driven by dyads with alpha and beta males; these dyads spent more time together in the

2011-12 study period, while dyads with gamma and subordinate males were very similar in both periods (Figure 2.2).

Dyads containing high-ranking males and dyads in the 2011-12 study period also spent more time in medium proximity (2-5m). The model containing only rank was the best fit (Table 2.3). There was moderate support for the second-ranked model which contained both rank and study period (Table 2.3).

Table 2.3

Time in proximity (n=176 dyads)

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

Table 2.3 Rank and study period best predicted time that dyads spent in close proximity, although there was also support for a model containing only rank. For time spent in medium proximity, the model containing only rank was the best fit.

Figure 2.2

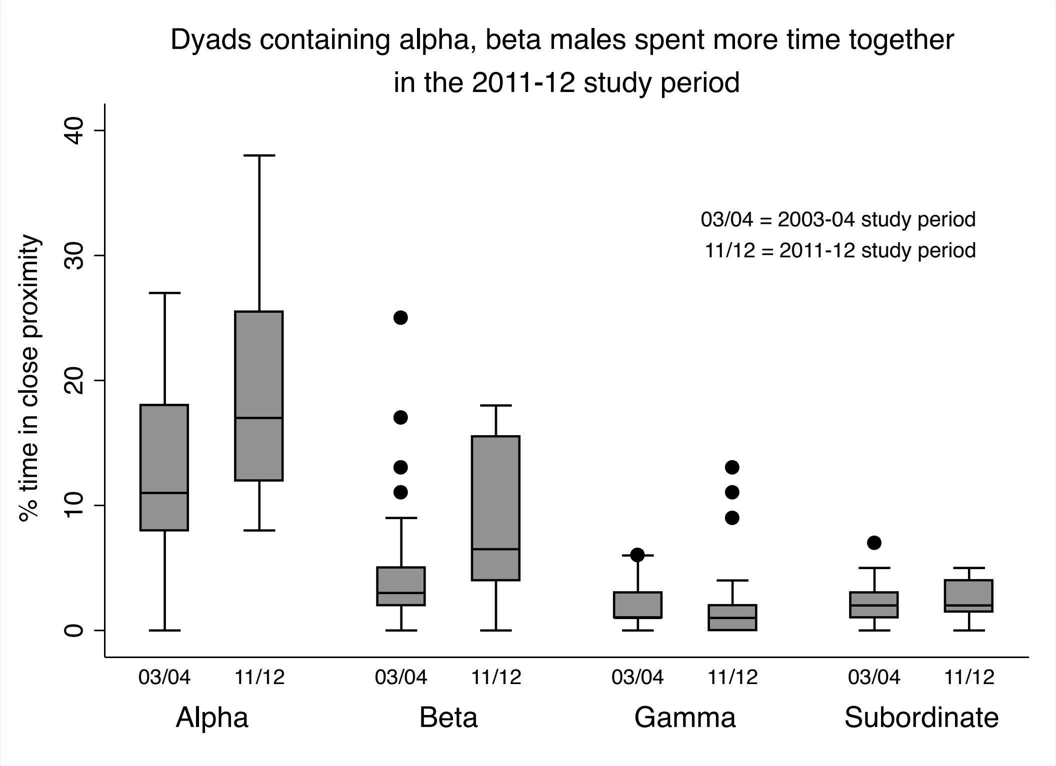

Figure 2.2 Dyads that included alpha and beta ranked males spent more time in close proximity in the 2011-12 dataset than in 2003-04. There were no differences in how much time dyads containing gamma and subordinate males spent in close proximity during the two study periods.

Proximity maintenance behaviors

Immatures worked harder to maintain proximity to higher-ranking males than lower-ranking ones (Table 2.4, Figure 2.3). They were also more likely to follow higher-ranking males, but we were only able to evaluate this in the 2011-12 study period (Table 2.4). The model containing male rank only was the best fit for both Hinde Index values and following (Table 2.4). Second-best models in both cases had ΔAICc of >5.

Table 2.4

Proximity maintenance behaviors

Hinde Index Values (n=94 dyads)	**Model**	**LL**	**K**	**ΔAICc**	**ωAICc**
	Rank	32.20	5	0	0.90
	β=0.095, SE=0.018				
Follow Rates (n=44 dyads)	Rank (***2011-12 period only)***	39.72	5	0	0.90
	β=0.071, SE=0.028				

Table 2.4 Male rank was the best predictor of both Hinde index values, a measure of proximity maintenance, and following rates (in the 2011-12 sample). Models containing other predictors had substantially lower AIC values.

Figure 2.3

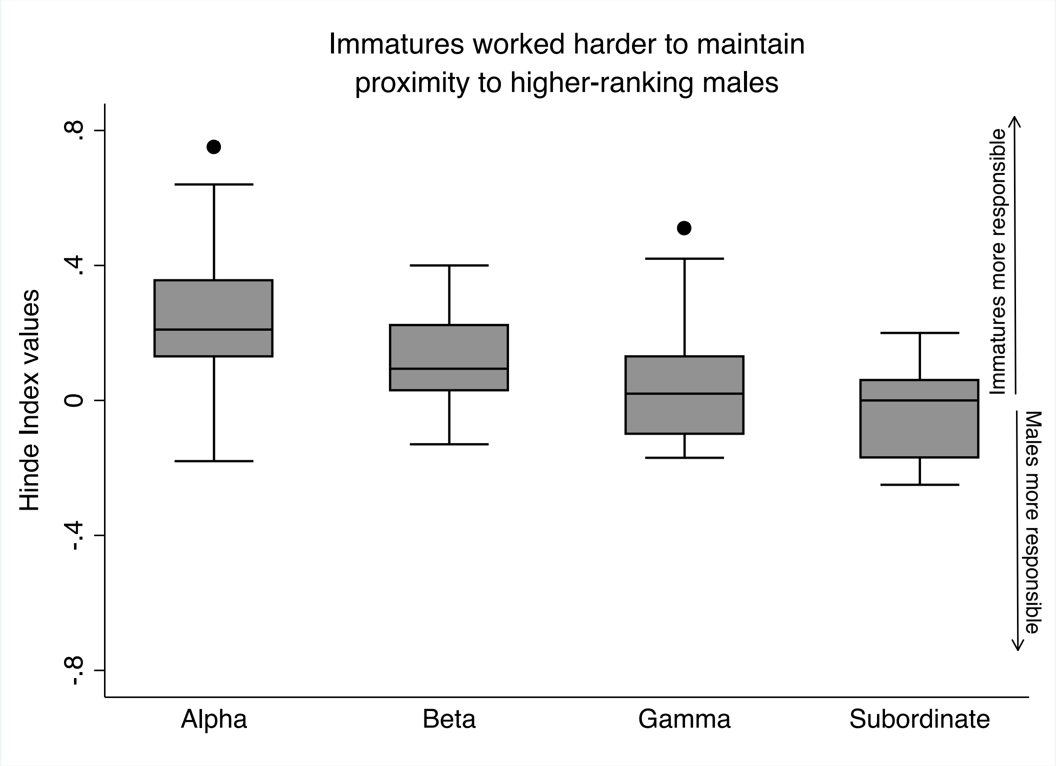

Figure 2.3 Hinde Index values, calculated from approach/leave interactions, for male-immature dyads. Higher values indicate immatures were more responsible for mainitaing proximity; lower ones indicate males were. Immatures worked harder to maintain close proximity to higher-ranked males than lower-ranked males.

Affiliative behaviors

Resting in contact and grooming: No one model clearly best fit the composite rest in contact/grooming scores (Figure 2.4). Two performed equally well: rank and study period, and rank/paternity/study period (Table 2.5). Once again, dyads with high-ranking males and dyads in the 2011-12 study period spent more time resting in contact and grooming. Two additional models had ΔAICc of <2 and performed similarly to each other: rank/age difference/study period, and a model containing all four predictors. The beta coefficient for age difference was negative, indicating 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 2.5). 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 (Figure 2.4).

Touching and social staring: Dyads containing high-ranking males touched and social stared more often. The rank-only model performed best for the composite touch/social staring measure (Table 2.5). Two other models performed similarly to each other and had ΔAICc of <2 (rank/paternity and rank/study period), but the ωAICc indicates that rank only is the best choice. Father/offspring dyads engaged in these behaviors less than unrelated dyads. High standard errors prevent reliable conclusions about the relationship between study period and touching/social staring (Table 2.5).

Playing: Dyads containing lower-ranking males played more than dyads that contained high-ranking males (Table 2.5). Models containing any other predictor variables had ΔAICcs of >6.

Table 2.5

Affiliation Measures (n=176 dyads)

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

Table 2.5 For resting in contact and grooming behaviors, four models containing combinations of all four predictor variables received similar support with AIC difference scores of <2. Touching and social staring were best predicted by rank, paternity, and study period. The model containing rank only was the best fit for play data.

Figure 2.4

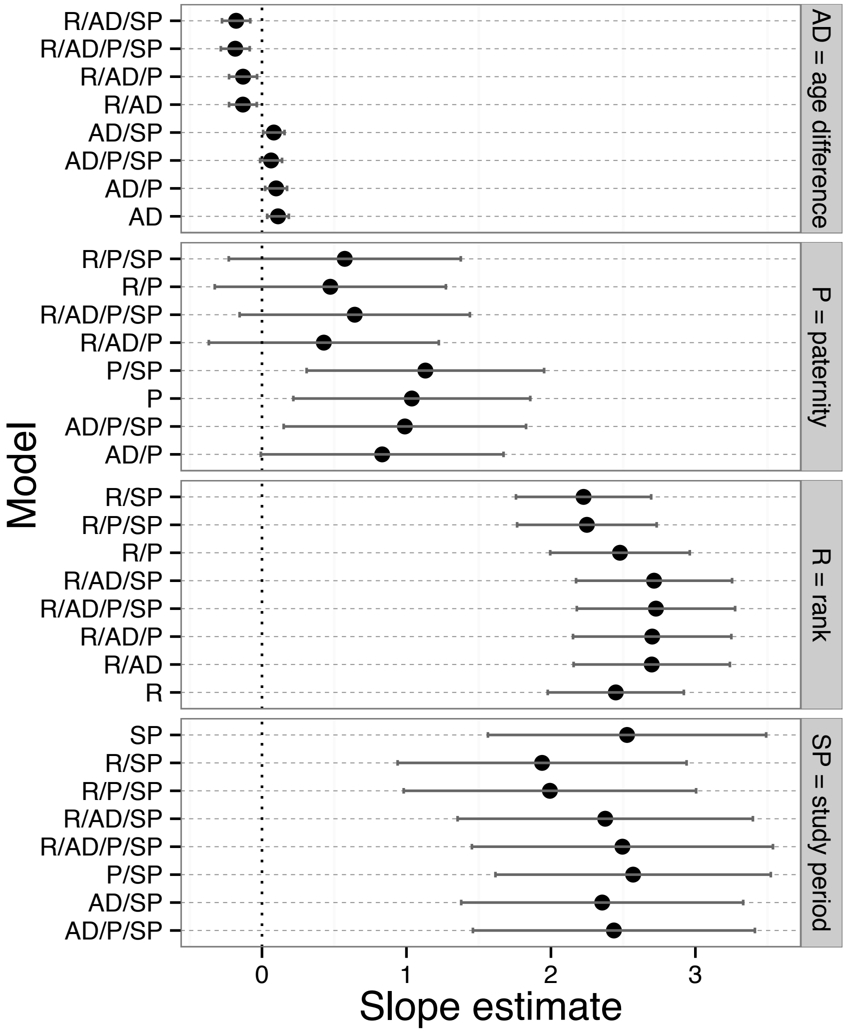

Figure 2.4 Change in beta coefficients and standard errors, by model, for composite rest in contact/groom scores. Left y axis contains all candidate models, grouped by predictor variable on the right hand y axis. Within predictor variable groups, models are arranged by AICc score from worst fit (highest AICc) to best (lowest AICc).

Aggressive behaviors

Rates of all types of aggression were extremely low, but 34 of 176 dyads (19%) engaged in at least one bout of vocal aggression. Only 11 of 176 (6%) engaged in at least one bout of non-contact aggression, which was the same number of dyads that had at least one instance of contact aggression.

Vocal aggression: Low-ranking males vocally aggressed toward their immature partners more often than high-ranking males (Table 2.6). Models containing any other predictor variable performed much worse (ΔAICc >8) than the rank-only model.

Non-contact aggression: High-ranking males directed non-contact aggression at immature partners more often than low-ranking males (Table 2.6). Again the model containing only rank performed far better than any other model; the second-best model had an ΔAICc > 9.

Contact aggression: Dyads in the 2003-04 study period engaged in more contact aggression than dyads in the 2011-12 study period (Table 2.6). The paternity-only model had an ΔAICc of < 2, but the standard error was larger than beta coefficient for both this model and the rank-only model (Table 2.6). The ωAICc indicates that the study period-only model is the best choice.

Table 2.6

Aggression (n=176 dyads)

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

Table 2.6 Rank was the best predictor of both vocal and non-contact aggression. Dyads in the 2003-04 study period engaged in more contact aggression. The models containing study period only and paternity only both received similar support.

Feeding tolerance

In the 2011-12 study period, dyads containing high-ranking males co-fed more than dyads with low-ranking males (Table 2.7). The rank-only model performed best. All other models had an ΔAIC >6.

Table 2.7

Feeding tolerance (n=44 dyads)

	Model	**LL**	**K**	**ΔAICc**	**ωAICc**
Co-feeding	Rank (***2011-12 period only)***	110.00	5	0	0.96
	β=0.013, SE=0.004				

Table 2.7 Rank was the best predictor of co-feeding behavior; males of higher rank were more tolerant of immatures feeding in close range.

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 multi-male groups, and two in a single-male group. In multi-male groups, males of all ranks carried and held infants. Ten males performed these behaviors, involving a total of 13 individual infants. Two alpha males accounted for 31 instances (60%), two beta males two instances (4%), one gamma male 12 (23%), and four subordinate males seven (13%). Twenty-eight of the 52 cases in multi-male 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.

Males tended to repeat the behavior with certain infants. One alpha male held or carried the same infant 26 times, but a similar-aged infant only once, although he was the father of both. The gamma male's 12 hold and carry behaviors were divided among only two infants (5 cases with one, 7 with the other) in spite of residing in a large group with many more infants available (~8). 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 his mother; the other mother/infant dyad remained in the main group.

"Fatherless" immatures

There were few differences in relationships of dyads whose fathers were present versus absent. They spent the same amount of time in close proximity, maintained proximity and followed at the same rate, rested in contact and groomed with males the same amount, played the same amount, received the same amount of non-contact and contact aggression, and co-fed with males at the same rate (Table 2.8). However, fatherless immatures received more vocal aggression than immatures with fathers, and spent more time in medium proximity to males than did immatures with fathers (Table 2.8).

Table 2.8

“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
Non-contact 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

Table 2.8 There were few differences in the behavior of dyads that contained immatures whose fathers were not co-resident and those whose fathers were. However, fatherless immatures received more vocal aggression, and spent more time in medium proximity to males.

Discussion

Results clearly demonstrate that male and immature mountain gorillas use rank, not paternity or age difference, to choose preferred social partners. Immatures spend more time near high-ranking males, work harder to maintain proximity to them, actively affiliate with them more, and feed in very close proximity to them more often than they do lower-ranking males. Behaviors that did not fit this pattern--play and vocal aggression--were still best predicted by male rank, but with the opposite effect; dyads containing low-ranking males were more likely to participate in these behaviors than those containing high-ranking males. Paternity had little predictive power in any domain, strongly suggesting males and immatures are unable to detect paternity in multi-male 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 emigrated later in pregnancy, it is unlikely these males ignored rather than failed to detect false paternity.

There are two reasons why gorillas may have failed to develop a more sophisticated kin discrimination system beyond male dominance rank: 1) if multi-male groups were rare in the species' evolutionary history, or 2) multi-male groups occurred regularly, but reproductive skew was high enough that dominance rank alone was a reliable paternity cue. That rank is such a strong predictor of social preference(s) may support the second scenario. If groups very rarely contained more than one adult male, then co-residence alone would be a sufficient paternity cue, and male-immature relationship quality might be expected to be widely distributed across all ranks of males. The strong predictive power of rank would instead imply that immatures regularly had a choice of more than one male social partner, but that rank was a very strong paternity predictor. Published paternity data from Karisoke's multi-male groups (Bradley et al. 2005 and the 2003-04 data presented here) demonstrate that reproductive skew is quite high even with multiple fully adult males in a social group.

The low skew observed in our 2011-12 sample may be a product of natural stochastic variation, with an aging dominant male of a large (40+) social group contributing to increased reproductive opportunities for younger, subordinate males. It is unlikely such conditions regularly appeared in *Gorilla beringei's* evolutionary history; if they had it seems probable there would have been selective pressure for more sophisticated mechanisms of paternal kin discrimination. Various authors have speculated about the length of the history of multi-male, multi-female grouping in mountain gorillas, and whether current conditions represent evolutionary disequilibrium (e.g. Stoinski et al. 2009b, Robbins et al. 2009, Robbins et al. 2013). 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 absolute numbers and high male:female ratios observed in the late 1990s and 2000s (Stoinski et al. 2009b, Cauillaud et al. 2014) appear to be a recent phenomenon. Our data support the notion that these groups are an evolutionarily novel configuration.

Both species of 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. Leutteneger & Kelly 1977, Harcourt et al. 1981, 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-to-body ratio via some other route. However, it is easy to conceive of this morphology developing in combination with a persistent minority of two or three-male groups with high reproductive skew, typically (though not always) made up of related males. Multi-male groups may have advantages for both females and males (Robbins 1995, Robbins et al. 2013), making it likely that these groups did not suddenly appear within the last 50 years of human observation. 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. in prep). Since paternal care behaviors 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.

This scenario is further supported by two other behavioral 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 (Stewart 2001, Rosenbaum et al. 2011, Rosenbaum et al. in prep). This is similar to the percentage of non-alpha sirings in both Bradley and colleagues (2005) data from the 1990s and more recent data. This suggests a form of behavioral bet-hedging, similar to the socializing patterns observed in male and female chacma baboons when females are lactating (Moscovice et al. 2010). Second, an evolutionary history that regularly included bi-male groups might help explain the remarkable behavioral 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' behavioral repertoire included tolerance of, and occasional cooperation with, other adult males.

Besides rank, the other notable predictor of our behavioral measures was study period; dyads in the 2011-12 sample spent more time near each other, actively affiliated more, and engaged in less contact aggression. It is probable that these differences are due to smaller groups sizes and/or male:immature ratio rather than differences in reproductive skew. Smaller groups are less spread out and move less, providing more opportunity for close proximity and active affiliation. Also, while the absolute ratio of males to immatures was similar in both study periods, the ratio of immature:dominant males (i.e., the most preferred males) was much higher in 2003-04. Overall ratio is likely irrelevant since not all males are equally preferred social partners. Since space near a single male is limited, immatures in 2003-04 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 a non-dominant male.

These data also provide further support for current theories of reproductive skew in mountain gorillas. Stoinski and colleagues (2009b) found support for a concessions model based on mating behavior, but lacked genetic paternity data. Our 2003-04 sample, where both the number of males per group and group size were considerably higher, had much higher reproductive skew than our 2011-12 sample. It would have been considerably harder for alpha males to police copulations in these larger groups with more competition, but their reproductive success is much higher than when the groups had fewer members and fewer 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 multi-male, multi-female 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 test predictions about the outcomes of evolutionarily novel social environments.

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Chapter 3

The effect of paternity certainty and infant mortality risk on maternal behavior toward silverback mountain gorillas (*Gorilla beringei beringei*)

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Abstract

Sexually selected infanticide is a common cause of infant mortality in mammal species when females lactate for longer than they gestate. Females employ anti-infanticide tactics across the entire reproductive cycle to minimize their losses. In species where males and females have long-term associations, male protection against infanticidal outsiders is a key component of their anti-infanticide strategy. Here we test whether mountain gorilla (*Gorilla beringei beringei*) mothers living in single and multi-male groups actively facilitate relationship development between their infants and a protective male, and what criteria females in multi-male groups use to choose a preferred male partner when they have a young infant. In single-male groups, where both infanticide risk and paternity certainty are highest, females with infants <1 year old spent more time near and affiliated more with adult males than females without young infants. In multi-male groups, maternal behavior toward males changed very little in the year after infant births. Females with young infants proportionally increased their time near males they previously spent little time with when compared to males they had previously preferred (p=0.052), perhaps to encourage paternity uncertainty and deter intra-group aggression. In these multi-male groups, infants inherited their mothers' male social partner preferences; 89% of 2-3 year old infants spent the most time in close proximity to the male that their mother had most preferred when they were <1. At this age, infants are still at risk of infanticide but moving independently, spending considerable time near males, and decreasing time near mothers. Females in multi-male groups use rank, not paternity, to choose a male social partner. Females may use a dual mating strategy, using rank to determine current fighting/protective ability while securing quality genes from males who will eventually rise in rank.

Introduction

According to the sexually selected infanticide hypothesis, males kill infants when the infant's death shortens the interval until the mother's next conception, and the infanticidal male is likely to sire the mother's next offspring (Hrdy 1979). In mammalian species in which the duration of lactation exceeds the duration of gestation, infanticide is common (van Schaik 2000). Sexually selected infanticide accounts for a high proportion of infant mortality in a variety of species, including gelada baboons (60%, Beehner & Bergman 2008); solitary southern sea lions (23%, Campagna et al. 1992); mountain gorillas (21%, Robbins et al. 2013); lions (27%, Pusey & Packer 1994); chacma baboons; (31-76%, Palombit et al. 2000); European rabbits (12%, Rodel et al. 2008); wolverines (32%, Persson et al. 2003); white-faced capuchins (43-68%, Perry 2012); and gibbons (83%, Borries et al. 2011). It is believed to be a major selective pressure in primates, carnivores, and rodents (reviewed in Ebensperger 1998, Janson & van Schaik 2000).

Female mammals use a variety of tactics to counter the threat of infanticide or reduce its impact on their lifetime fitness. These strategies are deployed across the full reproductive cycle, from the time of conception to weaning. In some species with promiscuous mating systems, females mate with multiple partners around the time of likely conception and during pregnancy in an apparent effort to confuse paternity (baboons: O'Connell & Cowlishaw 1994; patas monkeys: Enstam et al. 2002; Japanese macaques: Soltis et al. 2000; California ground squirrels: Boellstorff et al. 1994; bank voles: Kelmme & Ylönen 2009; reviewed in Clarke et al. 2009 & Palombit 2012). In others, females terminate pregnancies when infanticide risk is high (voles & mice: Bruce 1960, Stehn & Jannett 1981; gelada baboons: Mori & Dunbar 1985, Roberts et al. 2012; feral horses: Berger 1983). After birth, females use maternal aggression (e.g. ringtailed lemurs: Pereira & Weiss 1991; mice: Elwood et al. 1990), coalitional aggression (lions: Packer & Pusey 1983, Packer et al. 1990; chimpanzees: Newton-Fisher 2006; blue monkeys: Cords & Fuller 2010), avoidance of potentially infanticidal males (alpine marmots: Coulon et al. 1995; brown bears: Dahle & Swenson 2003; ursine colobus: Teichroeb et al. 2009), territoriality (white-footed and deer mice: Wolff 1985), or accelerated weaning (vervet monkeys: Fairbanks & McGuire 1987; baboons: Colmenares & Gomendio 1988) to reduce the risk to their infants. See Palombit (2012) for a review of counterstrategies against infanticide.

Agent-based models and empirical evidence strongly support the hypothesis that lasting associations between males and females are an evolved anti-infanticide strategy in both monogamous and promiscuous species (Stokes et al. 2003, Borries et al. 2011, Van Schaik & Kappeler 1997, Harcourt & Greenberg 2001, Opie et al. 2013, but see Lukas & Clutton-Brock 2013 for an alternative view on male-female relationships and infanticide). In monogamous systems, pair bonding across the entire reproductive cycle minimizes infanticide risk (e.g. Borries et al. 2011). In multi-male social systems, the primary function of relationships between males and lactating females is thought to be defense against infanticide. Female chimpanzees (e.g. Wrangham 1979 & 1993, Goodall 1986, Watts & Mitani 2000), lions (Packer & Pusey 1983, Bertram 1975), gorillas (Watts 1989, Harcourt & Greenberg 2001, Robbins et al. 2013), langurs (Borries et al. 1999) and baboons (Palombit et al. 1997, Palombit et al. 2000) all rely on resident males to protect infants from attacks.

In these promiscuous species, females may maintain close proximity to protective males in order to reduce the risk of infanticidal attacks by males who have recently immigrated into the group or gained high rank. In species in which females and their infants can benefit from male protection, females have incentive to encourage male behaviors that will protect offspring. Close male-female associations in baboons, often called “friendships” (Strum 1974, Smuts 1985, Silk 2002), appear to exist primarily for infant protection. These relationships emerge after infants are born (Palombit 2000, Palombit 2009) and are terminated after an infant dies (Palombit et al. 1997). Female baboons increase time spent with males after the birth of an infant, with the largest increase directed toward a primary male partner (Nyugen et al. 2009). These males are often, but not always, the fathers of their female friends’ infants (Moscovice et al 2010; Nguyen et al. 2009). Once infants become partially independent, they continue to benefit from these protective relationships. They maintain closer proximity to their genetic father when their mother is out of view and another male is nearby than when no other males are in proximity (Huchard et al. 2013).

Mountain gorillas (*Gorilla beringei beringei*) form one-male or multi-male groups in which male-female bonds are stronger than same sex bonds. In single-male groups, all females have close relationships with the resident male. In multi-male groups, females typically spend more time in proximity to certain males than others (Harcourt 1979, Watts 1992). In addition, most infants spend more time near some adult males than others once they move about independently (Stewart 2001, Rosenbaum et al.

2011). The primary function of such associations is thought to be infanticide avoidance (mountain gorillas: Watts et al. 1989, Harcourt & Greenberg 2001, Harcourt & Stewart 2007; western lowland gorillas: Stokes et al. 2003). Here, we evaluate whether female mountain gorillas modify their behavior after giving birth in ways that facilitate the close relationships observed between adult male and infant gorillas (e.g. Fossey 1979, Stewart 2001, Rosenbaum 2011).

In mountain gorillas, infanticide is most likely to happen after a new dominant male takes over (usually due to the death of a dominant silverback or a group disintegration), or during an encounter between two social units (Robbins et al. 2013). The situational risk of infanticide to a particular infant is dependent on group structure. Infants in single-male groups are much more likely to die after a dominant male replacement than infants in multi-male groups (57% of infants versus 6%; Robbins et al. 2013). During encounters between social units, risk to infants is similar in single male and multimale groups (5.5% of infants versus 2.0%, p=0.13; Robbins et al. 2013). Intragroup infanticide when a group male is likely the father is rare but has been reported (Robbins et al. 2013, Karisoke long-term records).

Protection from infanticide may not have historically been the only benefit male gorillas provided females and infants. Harcourt & Stewart (2007) have argued that although it is no longer a selective pressure in this population, protection from predation (specifically leopards) was once important. This view is bolstered by reports of predation in western gorillas (Fay et al. 1995, Robbins et al. 2004). Leopards are known to regularly prey on chimpanzees and bonobos (e.g. D'Amour et al. 2006, Boesch 1991). Female gorillas are similar in size to these species, so it is doubtful females could successfully defend infants on their own. A protective male who is 100% larger is likely the best defense. Multiple males might make a group a more intimidating target for a leopard, so it is possible that infants in single male groups were more likely to be killed by leopards.

Whether predation, infanticide, or a combination of the two were the primary driver(s) of male/female associations in this species, it is clear that females rely heavily on males to protect their infants regardless of group structure. In this paper we test the hypothesis that females actively facilitate the development of relationships between infants and adult males. We also evaluate the criteria mothers use to select a preferred male partner when their infants are young. Finally, we evaluate whether maternal preferences in their infants' first year of life is predictive of infants' association patterns when they are older.

Predictions

When an infant is born into a multi-male group, a mother could encourage the development of an exclusive relationship with a specific male, or encourage the development of relationships with several males. In both single and multi-male groups we expect that 1) females with new infants will spend more time near males than other females do (replicating Harcourt 1979); 2) females with new infants will spend more time actively affiliating (e.g. grooming, resting in contact) with male partners than other females do. Such behaviors facilitate familiarity and close contact between males and infants. In multi-male groups, 3) females with new infants will spend more time near a single male than other females do and 4) the male a mother spends the most time near during an infant's first year of life will be the male that infant spends the most time near when they are 2-3 years old. At this age, infants are still nursing and potentially vulnerable to infanticide, but independently mobile.

Females are expected to prefer males who are most able and willing to provide protection for their infants. Gorilla mothers are expected to display preferences for high-ranking males because they are likely to be the highest quality males (e.g. ursine colobus: Teichroeb et al. 2012; mountain gorillas: Robbins et al. 2013) *and* likely to be most willing to incur potential costs associated with defending infants. The willingness of males to protect infants should depend on the probability of paternity, and paternity may be at least partly based on male rank. In species like gorillas, in which there is a strong correlation between dominance and access to females, male rank provides a reliable reasonable proxy for paternity (e.g. long-tailed macaques: Engelhardt et al. 2006; savannah baboons: Alberts et al. 2003; mountain gorillas: Bradley et al. 2005; Verreaux's sifaka: Kappeler & Schaffler 2008). Although mountain gorillas in this population in the 1990's had relatively high reproductive skew (Bradley et al. 2005), more recent work indicates that skew may have fallen as both number of males in groups and male:female ratio has increased (Stoinski et al. 2009). However, high-ranking males still probably sire the majority of infants, so rank should still be an important cue.

Methods

Subjects and data collection

This study was conducted on the habituated mountain gorilla population monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center (KRC), located in Volcanoes National Park, Rwanda. Data were collected by the first author (in 2003-04 and 2011-12) and second author (in 2011-12) via 50-minute focal animal follows on adult males, plus extracted from the KRC long-term database whenever protocol overlap allowed. Long-term KRC data were collected between 2003 and 2013 by a variety of observers who passed repeated inter-observer reliability tests, also using 50-minute focal animal follows on adult males and adult females. All focals included 10-minute proximity scan samples, where the identification of all animals within 2m of the focal subject was recorded.

Maternal categories

Mothers with infants 0-12 months old are considered mothers with young infants. Infants are much more reliant on their mothers in their first year than second. Before 6 months of age they virtually never move independently, but around 10 months old they begin spending progressively more time on substrates other than their mother, moving >5m away from her, and drastically increasing their range of locomotor activities to include climbing and rolling down hills (Fletcher 2001, Doran 1997). Spending more time away from their mothers coincides with the beginning of the sharp increase in time infants spend with adult male(s), as described in Stewart (2001) and Rosenbaum et al. (2011). Parous adult females with offspring older than 12 months or without living offspring are referred to as either 'other females' or 'females without young infants.'

Our sample contains 35 parous adult females (12 in single-male groups and 23 in multi-male). All females contributed proximity data both when they were mothers of young infants and when they were not, so proximity analyses consist solely of paired data. This study takes advantage of various protocols where not all dyads contributed to all behaviors in both female conditions, so analyses for other behaviors include both paired and unpaired data. Sample sizes are reported for each analysis in the relevant table. To control for group composition, we only used paired data from the same male/female dyad for time periods in which basic group composition was stable. For example, data were not compared before and after group splits in cases where a dyad remained co-resident. Minor composition changes such as dispersal of a peripheral male or a different female were not considered. For continuous data, each male/female dyad needed a minimum of 10 hours of observation time over a 6-month period both when they had young infants and when they did not to be included in the analyses (mothers of young infants: mean=39.65 hours, min=10.67, max=85.67; other females: mean=26.68 hours, min=10.43, max=74.52). For proximity data, each dyad needed to have at least 100 scans taken at 10-minute intervals for each condition (mothers of young infants: mean=385 scans, min=103, max=1758; other females: 373 scans, min=109, max=989).

Male categories

Adult males (hereafter referred to as silverbacks) were included if they were at least 12 years old at the earliest time that data were collected for female(s) in their group (n=19 silverbacks). This follows age/sex classifications outlined in Watts & Pusey (1993). Although 12-year old males are not yet at their maximum size (Watts 1990, Harcourt 1981), they copulate with adult females, can sire offspring (Bradley et al. 2005), and take an active role in intergroup interactions, a time when infanticide risk is high (e.g. Watts 1989 & 1991, Sicotte 2001, Robbins 2003).

Group structure

Our analyses include two single-male groups, four multi-male groups, and a two-male group that was functionally single-male because the beta male so rarely interacted with females. In 2011-12, during 49 hours of focal follow data collection, he interacted with females only nine times. Eight interactions were aggressive and took place from a distance, and one was an approach/leave interaction. He was never observed copulating. This silverback was removed from the analysis and the group is considered single-male for purposes of these behavioral analyses. For the analyses that use paternity and rank to evaluate maternal and infant preference criteria in multi-male groups, we included infants and their mothers from this group.

One of the four multi-male groups contained between four and seven silverbacks at different points in time, with thirteen individual silverbacks residing in the group over the course of the analyzed time period. Most of our data come from 2003-04 and 2011-12. Six silverbacks that turned 12 years old between 2005 and 2010 are included only for specific analyses because they did not co-reside with the mother/infant pairs for whom we had adequate data. All of these males left the group either before data collection began in 2011, or slightly after. In this group the dominant silverback remained the same throughout, and paired data from when females did and did not have young infants is only compared when the silverback partner in question occupied the same dominance rank during both conditions.

Two other multi-male groups also changed composition. One contained three silverbacks for part of the study, and two for the remainder after a former dominant silverback left the group. Dyads containing this silverback are only compared across conditions when he was dominant for both. Another four-male group lost a third-ranking male when he dispersed to become a lone silverback; he was only included as a subject when he was co-resident with the relevant females for both conditions.

Behavioral measures

We evaluated five behavioral variables between silverbacks and adult females: approach/leave interactions, time spent in close proximity, resting in physical contact, grooming, and following (see Table 3.1 for definitions). We used proximity data to determine if infants aged 2-3 years (hereafter referred to as 2 year olds) preferred the same silverback that their mother spent the most time with when they were <1 year old.

Table 3.1 Behavioral definitions

Behavior	Definition	Directional?	Method
Approach/ leave	One animal moves within 2m of another animal, and stays at least 5 sec; one animal moves outside of 2m range after staying at least 5 sec	Yes	CFS*
Time in 2m proximity	Within 2m of another animal, regardless of activity	No	ISS^
Groom	One animal manipulates another's pelage with mouth or fingers	Yes	CFS
Rest in contact	One animal rests any body part on any part of another's body for at least 5 sec	When observed	CFS
Follow	Individual gets up and walks directly in the path of an individual leaving a resting or feeding space. Must be within 2m and 5 sec of the first animal leaving; must walk in path for at least 5m.	Yes	CFS

*CFS=Continuous focal animal sampling; ^ISS=Instantaneous scan sampling

Genetic paternity

Fecal samples were collected from all infants, mothers and potential fathers for noninvasive genetic paternity analysis. Samples were preserved using the two-step ethanol-silica storage method described in Nsubuga et al. (2004). We extracted DNA and genotyped samples at 16 autosomal microsatellite loci using the approach detailed in Arandjelovic et al. (2009), including the appropriate amount of replication of results to avoid errors such as allelic dropout. Sex was determined or confirmed using a PCR-based sexing assay (Bradley et al., 2001).

Individual IDs of samples were confirmed by comparing genotypes of known mother/infant pairs or by comparing the genotypes obtained from two or more samples purporting to be from the same individuals. We considered as potential sires all males 7 years of age or older resident in the group at the time of conception (Bradley et al., 2005). There were one to 14 potential sires per offspring (average 5.8). We conducted likelihood assessment of paternity using CERVUS 3.0.3 (Kalinowski et al., 2007). Thereby we conducted simulations assuming either 5 or 9 potential sires and assuming that 10% of potential sires were related at the level of half-siblings (R=0.25). The simulations assuming 5 and 9 potential sires were applied to datasets consisting of offspring with 6 or fewer potential sires and 7 or more potential sires per offspring, respectively. Results did not differ when we used simulations with different numbers of potential sires or increased proportions of relatives among the potential sires. In addition to employing CERVUS to assess the statistical confidence of the paternity assignments, we 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 in (Vigilant et al., in prep).

Two of the 18 infants for which we were able to determine paternity were sired by males in groups other than the one where they resided during data collection. In both cases, their mothers had transferred social groups early in the pregnancy.

Data summary

Behavioral data were summarized separately for every silverback/female dyad during times in which each female had young infant and when she did not. We also summarized proximity scan data for each silverback/infant dyad when the infant was two years old. For one analysis we summarized the proportion of time females in multi-male groups spent in proximity to all available males, by summing the percentage of time she spent with each male both when she did and did not have a young infant.

<u>Behavioral measures</u> We calculated the proportion of time dyads spent in proximity by dividing the number of instantaneous scans in which the dyad partner appeared by the total number of in-view scans collected on both dyad partners. Grooming and resting in contact were calculated as a percentage of total time both animals were observed. Approach, leave, and following rates were calculated as the

number of times the behavior was observed divided by the amount of time visible. We also calculated the proportion of approaches and leaves females were responsible for in each dyad if the dyad had $\geq$ 15 approach/leave interactions.

Partner diversity To determine whether females in multi-male groups showed differences in partner diversity when they did and did not have young infants, we calculated Shannon-Weiner index values (*H*) for all females in multi-male groups (Dunbar 1984):

$$H = -\Sigma[(p_i) \times \ln(p_i)]$$

Where p_i is the amount of time a female spent in 2m proximity to silverback *i*, divided by the total time spent in 2m proximity to all available silverbacks. We used *H* to calculate an equitability score *E* (Pielou 1969):

$$E = H'/H_{max}$$

where H_{max} is the number of silverbacks available to a female. Values closer to zero indicate that females distributed their time less equally across silverbacks; values closer to one indicate they distributed their time more equally. *E* scores were summed for all mothers of young infants and other females separately.

We also calculated whether females' change in time spent with silverbacks when they had young infants varied depending their relative preference for him versus other silverbacks when they did not have young infants. In multi-male groups, we ranked all silverbacks available to each female by the amount of time spent with him when they did not have a young infant. If a female spent the same amount of time with two silverbacks, they both received the same rank. We grouped silverbacks by these "female choice" rankings. We then calculated the mean percent change in time across all dyads that held the same female choice rank, to determine if females changed their time spent in close proximity to one or more ranks of these silverbacks than to others.

Three females had data from two different points in time for both conditions (i.e., after the births of two different infants, and then again after those infants had aged past one year). We counted each of these as separate occurrences in our data summary. Thus, the total number of females in multi-male groups for these analyses is 23, but the total number of data points is 26 for each female condition.

Silverback dominance rank For some analyses, silverbacks are grouped by dominance rank. Based on displacement patterns, they were categorized as alpha (rank 1, referred to here as dominant), beta (2), gamma (3), and subordinate (>3) following Stoinski & colleagues (2009) method. In one case we used an Elo rating (Neumann et al. 2001) to determine the date of a dominance change between a dominant and second-ranked silverback. In general, older males are dominant over younger ones.

Data analysis

It was clear from visual inspection of the data that patterns for dyads containing dominant silverbacks were quite different than patterns for dyads with non-dominant silverbacks. We separated the two categories of silverbacks for most analyses and present them separately here, unless otherwise stated.

To determine if female condition, group type, and in some cases male rank were related to our behavioral measures, we used multi-level mixed-effect regression models. If the female was the unit of analysis, we used her ID as a random effects parameter, and if the dyad was the unit, both partner's IDs were included as random effects to control for the repetition of IDs across dyads. To compare the mean of equitability scores, we used a paired t-test.

To determine what metric females use to choose their silverback partner(s), we calculated adjusted Akaike information criteria (AICc) scores for mixed-effects, multi-level poisson regression models (because variables were based on count data). We evaluated models containing silverback dominance rank and genetic paternity individually, both variables together, and an interaction between the two predictors for silverbacks' female choice ranks. These were ordered according to AICc score. We then calculated AICc weights to evaluate the relative importance of dominance rank and paternity (Anderson & Burnham 2002, McElreath et al. 2008). All analyses were performed using Stata 13.

Results

Prediction 1: Females with young infants will spend more time near dominant males than other females do.

Dominant silverbacks

Time in proximity: Females in single-male groups spent more time on average near dominant silverbacks when they had young infants (mean=23.7%, SD=5.1%) than when they did not (mean=14.1%, SD=7.8%, n=12 dyads per condition). Females in multi-male groups spent the same amount of time with dominant silverbacks whether or not they had young infants (females with young infants: mean=4.9%, SD=5.7%; other females: mean=4.1%, SD=4.9%, n=102 dyads per condition). Females in single-male groups spent more time near dominant silverbacks than females in multi-male groups did across both conditions (Table 3.2, Figure 3.1).

Figure 3.1

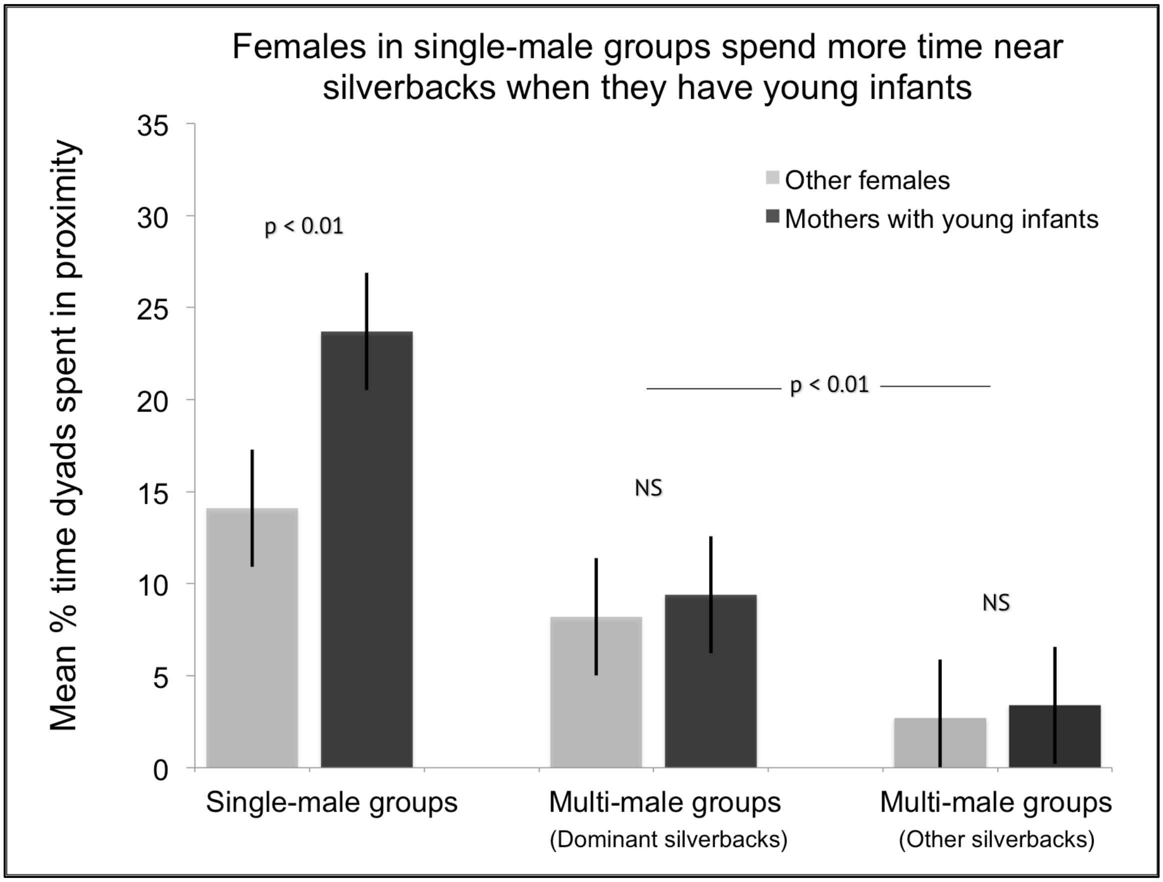

Figure 3.1 Only females in single-male groups spent more time near adult males when they had new infants. Females in multi-male groups spent more time with dominant males than non-dominant males, but spent the same time near both types regardless of whether they had young infants.

Rate of proximity initiation: In both single and multi-male groups, females with young infants approached dominant silverbacks at significantly higher rates (mean=0.23/hour, SD=0.16, n=22) than other females (mean=0.16/hour, SD=0.11, n=35 dyads) (Table 3.2). Females in single-male groups also approached dominant silverbacks at significantly higher rates than females in multi-male groups regardless of condition (single male groups: mean=0.28/hour, SD=0.14, n=15 dyads; multi-male groups: mean=0.16/hour, SD=0.12, n=42 dyads) (Table 3.2).

We had information on approach rates for females with young infants in single male groups for three dyads. They approached silverbacks a mean of 0.46 times/hour (SD=0.10). For other females in single-male groups, the mean approach rate was significantly lower, 0.23/hour (SD=0.10, n=12 dyads; β=0.168, SE=0.042, z=4.02, p=0.000). In multi-male groups, females with young infants also approached dominant silverbacks more often (0.19/hour, SD=0.14, n=19 dyads) than did other females (mean=0.12, SD=0.10, n=23 dyads; β=0.072, SE=0.030, z=2.37, p=0.018). Females in single male groups trended toward increasing their approaches to dominant silverbacks more when they had young infants than females in multi-male groups in either condition did (Table 3.2).

Rate of proximity termination: Females with young infants in both group types left dominant silverbacks at the same rate as other females (with young infants: mean=0.16/hour, SD=0.10, n=22 dyads; other females: mean=0.14/hour, SD=0.10, n=35 dyads) (Table 3.2). In both conditions, females in single-male groups left dominant silverbacks at higher rates than females in multi-male groups did (single male groups: mean=0.23/hour, SD=0.11, n=15 dyads; multi-male groups: mean=0.12/hour, SD=0.09, n=42 dyads) (Table 3.2).

In our small sample from single male groups there was no difference in the rate at which females with young infants and other females left dominant silverbacks (with young infants: mean=0.30, SD=0.11, n=3 dyads; other females: mean=0.21/hour, SD=0.10, n=12 dyads; β=0.092, SE=0.068, z=1.34, p=0.180). These values were not different than values in multi-male groups for females with young infants and other females, who also did not leave dominant silverbacks at different rates (females with young infants: mean=0.14/hour, SD=0.09, n=19 dyads; other females: mean=0.11/hour, SD=0.09, n=23 dyads; β=0.033, SE=0.025, z=1.31, p=0.191) (Table 3.2).

Table 3.2 (Dyads containing dominant silverbacks)

Time, 2m prox	Coef.	Std. Err.	Z	P>|z|	95% CI (lower)	95% CI (upper)	n (dyads)
Female condition	0.096	0.021	4.60	0.000	0.055	0.137	MYI*=38 OF^=38
Group type	-0.057	0.020	-2.83	0.005	-0.097	-0.018	Single male=24 Multi-male=52
Fem condition* Group type	-0.084	0.025	-3.33	0.001	-0.133	-0.035	
Constant	0.140	0.017	8.34	0.000	0.107	0.173	
Rate, female approaches							
Female condition	0.198	0.063	3.13	0.002	0.074	0.321	MYI=22 OF=35
Group type	-0.110	0.039	-2.79	0.005	-0.187	-0.033	Single male=15 Multi-male=42
Fem condition* Group type	-0.125	0.069	-1.81	0.070	-0.261	-0.010	
Constant	0.228	0.032	7.13	0.000	0.166	0.291	
Rate, female leaves							
Female condition	0.091	0.059	1.55	0.122	-0.024	0.207	MYI=22 OF=35
Group type	-0.096	0.033	-2.92	0.003	-0.160	-0.031	Single male=15 Multi-male=42
Fem condition* Group type	-0.057	0.066	-0.87	0.383	-0.186	0.071	
Constant	0.205	0.027	7.72	0.000	0.153	0.257	

*MYI=mothers of young infants; ^OF=other females.

Table 3.2 Females in single-male groups, especially those with young infants, spent more time near dominant silverbacks and approached them more often than females in multi-male groups. In multi-male groups there was no difference in how much time females with young infants and other females spent near dominant silverbacks. However, females with young infants in multi-male groups approached dominant silverbacks more often than other females did.

Non-dominant silverbacks in multi-male groups

Time in proximity: Females spent significantly less time near non-dominant silverbacks than dominant ones (non-dominant silverbacks: mean=3.1%, SD=4.4%, n=152 dyads; dominant silverbacks: mean=8.8%, SD=5.5%, n=52 dyads; Figure 3.1). There was no difference in the proportion of time females with young infants and other females spent in proximity to non-dominant silverbacks (females with young infants: mean=3.4%, SD=4.8%; other females: 2.7%, SD=3.9%, n=76 dyads per condition; Figure 3.1). Females overall spent more time with higher-ranking non-dominant silverbacks than lower-ranking ones (β=-0.024, SE=0.004, z=5.29, p<0.000, n=52 β silverback dyads, γ dyads=50, δ dyads=50).

Rate of proximity initiation: Rates of female approaches to non-dominant silverbacks were generally low. However, there was a trend for females with young infants to approach non-dominant silverbacks more frequently (0.08/hour, SD=0.12, n=43 dyads) than other females did (0.06/hour, SD=0.10, n=56 dyads; β=0.025, SE=0.089, z=1.89, p=0.059). Females approached higher-ranking non-dominant silverbacks at significantly higher rates than they approached lower-ranking ones in both conditions (β=-0.038, SE=0.013, z=3.04, p=0.002, n=39 β silverback dyads, γ dyads=37, δ dyads=23).

Rate of proximity termination: Rates of females leaving non-dominant silverbacks were also very low, but again there was a trend for females with young infants to leave more frequently than other females did (with young infants: mean=0.09/hour, SD=0.13, n=43 dyads; other females: mean=0.06/hour, SD=0.10, n=56 dyads; β=-0.030, SE=0.017, z=1.71, p=0.087). Again, females left animals of higher rank more often than animals of lower rank (β=-0.033, SE=0.015, z=2.23, p=0.026, n=39 β silverback dyads, 37 γ dyads, 23 δ dyads).

Since we found no change in the amount of time females spent near either dominant or non-dominant silverbacks in multi-male groups when they had new infants, we also checked to see whether their overall time near all males changed. When the data is grouped by female rather than silverback/female dyad, females' time near all silverbacks was the same regardless of whether they had young infants (with young infants: mean=0.19, SD=0.09, min=0.05, max=0.42; other females: mean=0.16, SD=0.07, min=0.06, max-0.32; β=0.356, SE=0.263, z=1.36, p=0.175, n=26).

Change in time in close proximity (all dyads)

Females with young infants showed the largest increase in time near the silverbacks they had spent the least time with when they did not have young infants (p=0.052; Figure 3.2, Table 3.3). The 4th-choice dyads contained an outlier whose time together jumped from 0% when the female did not have a young infant to 11% when she did, but even with this dyad removed a trend remains (Table 3.3). There were insufficient approach/leave interactions to evaluate which partner was primarily responsible for this result.

Table 3.3 (All dyads in multi-male groups)

Mean % change, time in 2m proximity	**Coef.**	**Std. Err.**	**Z**	**P>|z|**	**95% CI (lower)**	**95% CI (upper)**	**n (dyads)**
Female choice rank	0.012	0.006	1.94	0.052	-0.000	0.024	α=30, β=29 γ=28, δ=12
SB dominance rank (**all**)	-0.010	0.005	-1.91	0.056	-0.021	-0.000	α=23, β=26 γ=25, δ=25
Constant	0.007	0.012	0.61	0.541	-0.016	0.030	
Mean % change, time in 2m proximity (OUTLIER REMOVED)							
Female choice rank	0.010	0.006	1.71	0.086	-0.001	0.022	α=30, β=29 γ=28, δ=11
SB dominance rank (**all**)	-0.012	0.005	-1.99	0.046	-0.021	-0.000	α=23, β=26 γ=25, δ=24
Constant	0.010	0.012	0.86	0.389	-0.013	0.033	

Table 3.3 Females with young infants increased their time near silverbacks they spent little time with previously more than they increased their time near previously preferred silverbacks.

Figure 3.2

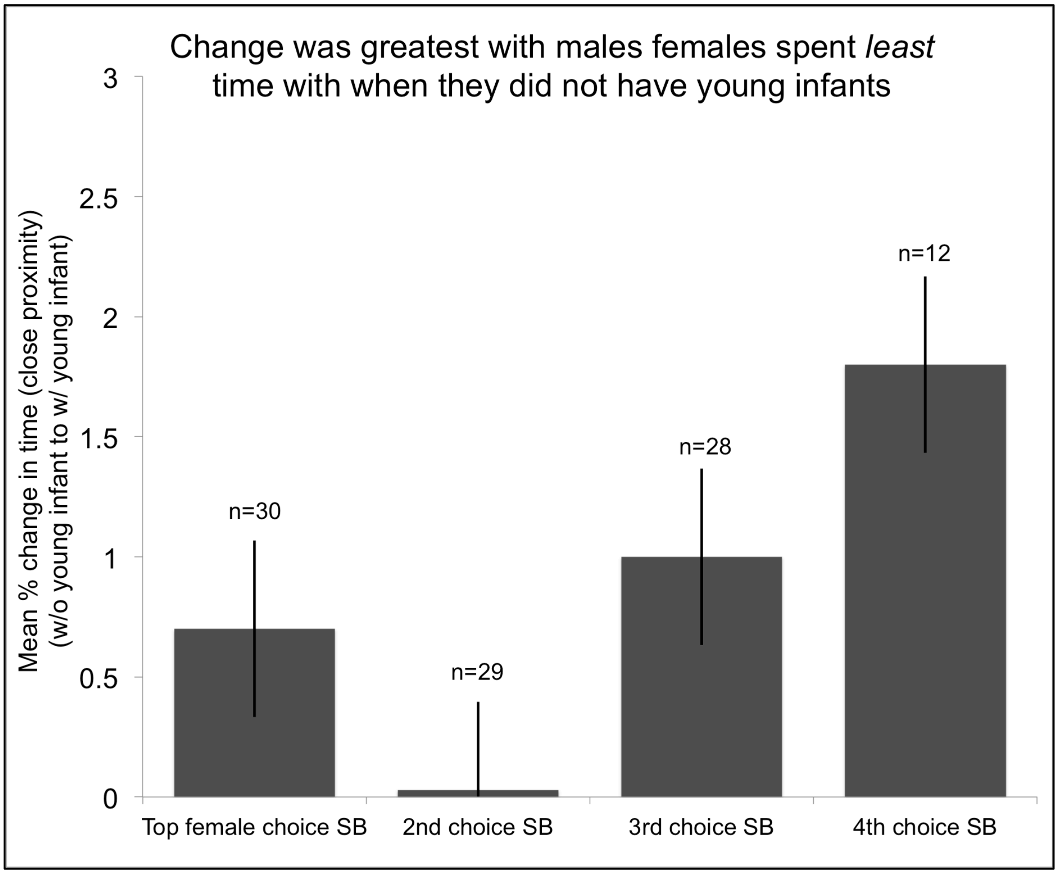

Figure 3.2 Females with young infants increased their time near silverbacks they spent little time with previously more than they increased their time near previously preferred silverbacks.

Prediction 2: Females with young infants will spend more time actively affiliating with silverback partners than other females do.

Dominant silverbacks

Resting in contact: Females with young infants in single-male groups spent far more time resting in contact with dominant silverbacks (4.3% and 10.4% for n=2 dyads) than did other females in single-male groups (mean=1.0%, SD=1.1%, n=12 dyads) or females in either condition in multi-male groups (females with young infants: mean=1.0%, SD=2.1%, n=16 dyads; other females: mean=1.0%, SD=1.0%, n=19 dyads). The sample of females with young infants in single male groups is very small, but despite this the result is highly significant (Figure 3.3a, Table 3.4).

Figure 3.3a

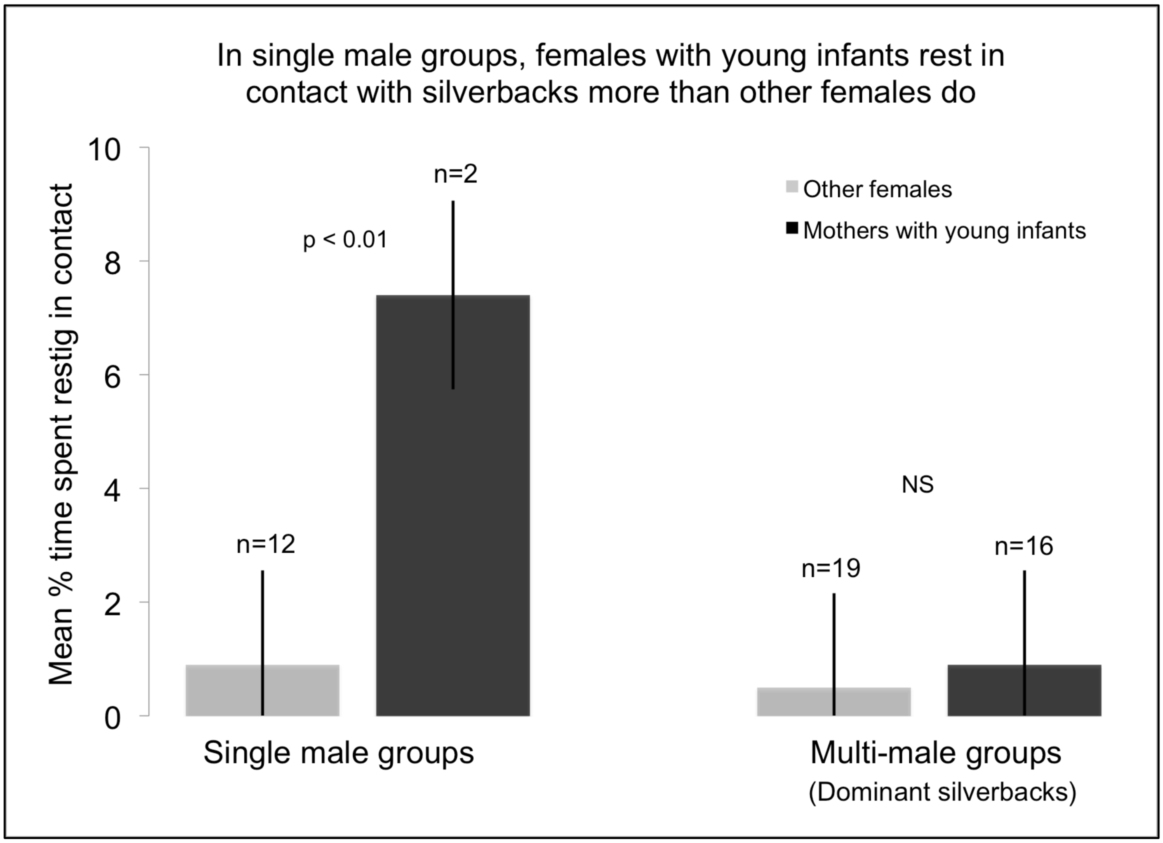

Figure 3a Females in single male groups quadrupled their time spent resting in contact with adult males when they had young infants; females in multi-male groups did not.

Grooming: Grooming results were very similar to results for resting in contact. Females with young infants in single-male groups spent much more time grooming with males (0.1% and 3.8% for n=2 dyads) than other females in single-male groups did (mean=0.3%, SD=0.8%, n=11 dyads), or their counterparts in either condition in multi-male groups (females with young infants: mean=0.08%, SD=0.3%, n=19 dyads; other females: mean=0.05%, SD=0.1%, n=25 dyads). Again, these results are highly significant despite the small sample (Figure 3.3b, Table 3.4).

Figure 3.3b

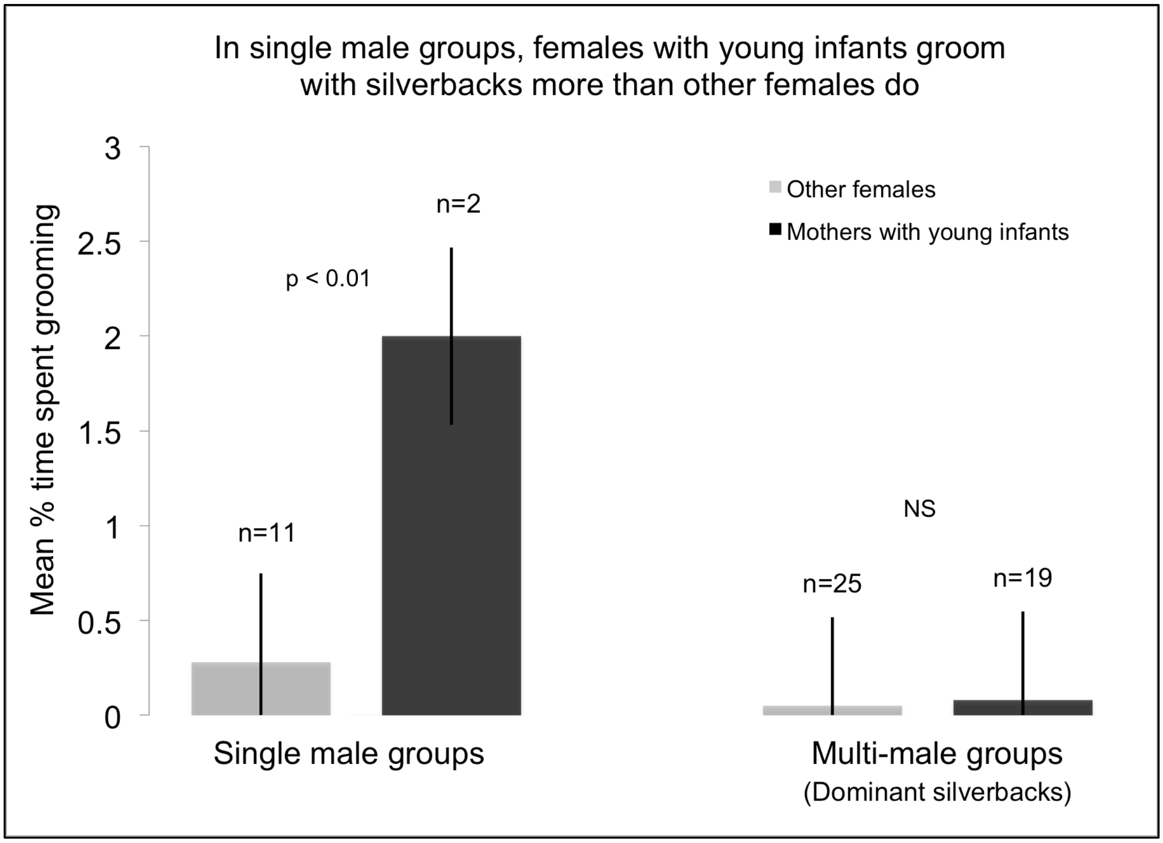

Figure 3.3b Females in single male groups also quadrupled their time spent grooming with adult males when they had new infants; females in multimale groups did not.

Following: Following results were also very similar to grooming and resting in contact; females with young infants in single-male groups performed the most follows (mean=0.11/hr, SD=0.04, n=3 dyads). However, rates of following in single male groups for both mothers of young infants and other females (mean=0.07/hr, SD=0.05, n=12 dyads) were also higher than following rates in multi-male groups in either condition (females with young infants: mean=0.02/hr, SD=0.03, n=19 dyads; other females: mean=0.02/hr, SD=0.03, n=23 dyads; Figure 3.3c, Table 3.4).

Figure 3.3c

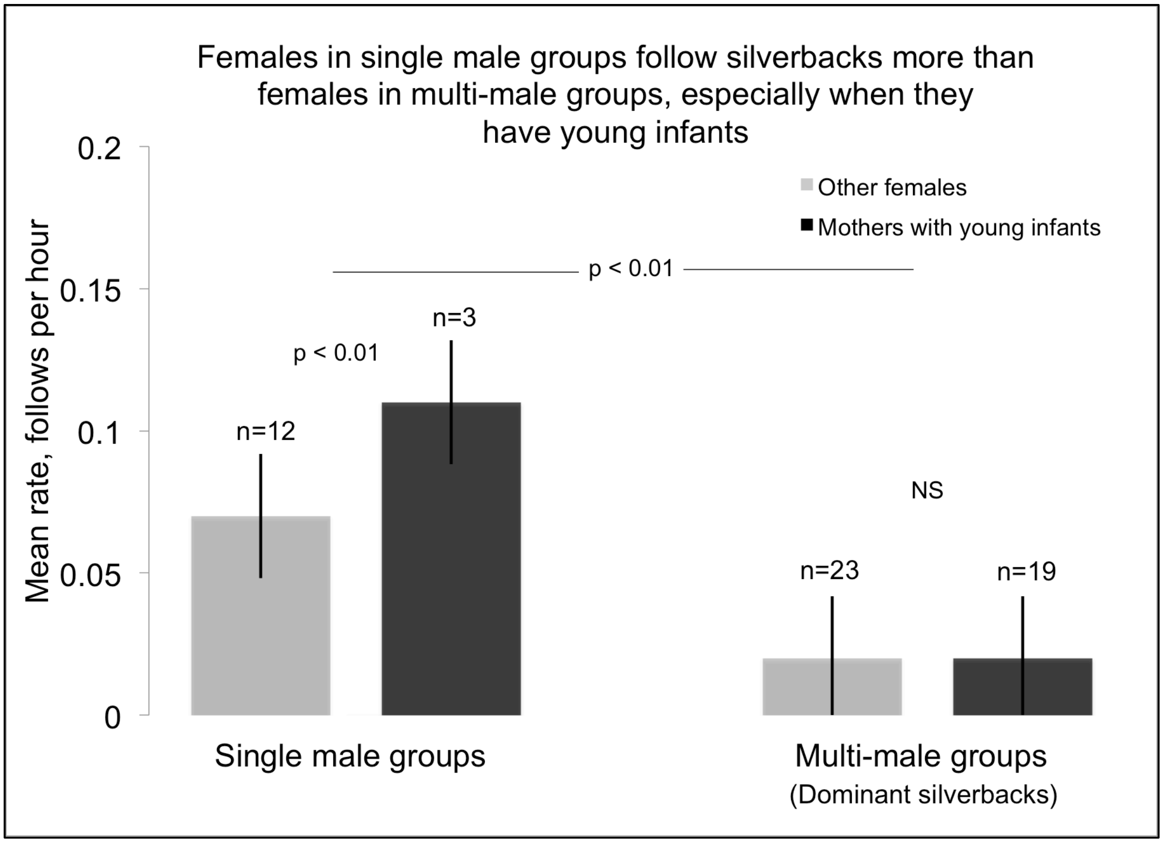

Figure 3.3c Females in single male groups followed males more than females in multi-male groups followed dominant males. They also followed males more often when they had young infants than when they did not.

Table 3.4 (Dyads containing dominant silverbacks)

% time rest in contact	Coef.	Std. Err.	Z	P>|z|	95% CI (lower)	95% CI (upper)	n (dyads)
Female condition	0.063	0.010	6.32	0.000	0.044	0.083	MYI=18 OF=31
Group type	0.006	0.012	0.53	0.594	-0.017	0.030	Single male=14 Multi-male=35
Fem cond*Grp type	-0.060	0.011	-5.46	0.000	-0.082	-0.038	
Constant	0.007	0.009	0.86	0.392	-0.010	0.025	
% time grooming							
Female condition	0.011	0.003	3.98	0.000	0.006	0.017	MYI=21 OF=36
Group type	0.000	0.003	0.00	0.996	-0.005	0.005	Single male=13 Multi-male=44
Fem cond*Grp type	-0.011	0.003	-3.71	0.000	-0.017	-0.005	
Constant	0.001	0.002	0.40	0.690	-0.003	0.005	
Follow rate							
Female condition	0.051	0.021	2.47	0.013	0.011	0.091	MYI=22 OF=35
Group type	-0.046	0.012	-3.71	0.000	-0.071	-0.022	Single male=15 Multi-male=42
Fem cond*Grp type	-0.049	0.023	-2.17	0.030	-0.093	-0.005	
Constant	0.063	0.010	6.22	0.000	0.043	0.083	

Table 3.4 Females with new infants in single-male groups increased their time spent resting in contact and grooming with silverbacks, and followed them more often.

Non-dominant silverbacks

Resting in contact: There was no difference in the amount of time females with young infants and other females spent resting in contact with non-dominant silverbacks (with young infants: mean=0.20%, SD=0.53, n=41 dyads; other females: mean=0.20%, SD=0.80, n=50 dyads; β=-0.001, SE=0.001, z=0.18, p=0.855). Male rank did not predict percent time spent resting in contact (β=-0.004, SE=0.004, z=1.13, p=0.257, n=35 β silverback dyads, 34 γ dyads, 22 δ dyads).

Grooming: There was also no difference in the amount of time females with young infants and other females spent grooming with non-dominant silverbacks (with young infants: mean=0.03%, SD=0.15, n=40 dyads; other females: mean=0.22%, SD=1.6, n=66 dyads; β=0.002, SE=0.002, z=1.27, p=0.203). Male rank did not predict percent time spent grooming (β=-0.002, SE=0.003, z=0.55, p=0.586, n=41 β silverback dyads, 39 γ dyads, 26 δ dyads).

Following: Females with young infants and other females followed non-dominant silverbacks at similar rates (with young infants: 0.01/hour, SD=0.03, n=43 dyads; other females: 0.01/hour, SD=0.04, n=56 dyads; β=-0.003, SE=0.007, z=0.55, p=0.581). Male rank did not predict following rate (β=-0.010, SE=0.009, z=0.98, p=0.327, n=39 β silverback dyads, 37 γ dyads, 23 δ dyads).

<u>Prediction 3</u>: In multi-male groups, females with young infants will spend more time near a single silverback than other females do.

Individual females demonstrated substantial variability in their association patterns with silverbacks. Some were continuously distributed, some were uni- or bi-modal, and a few were relatively flat with little difference in amount of time spent with individual males. While some females had similar distributions when they both did and did not have young infants, others showed marked differences between conditions (see Figure 3.4 for representative examples). Despite this, equitability scores for the two conditions were very similar (with young infants: mean=0.194, SD=0.100, n=31; without young infants: mean=0.189, SD=0.094, n=31; *t*=0.308, p=0.761).

Figure 3.4

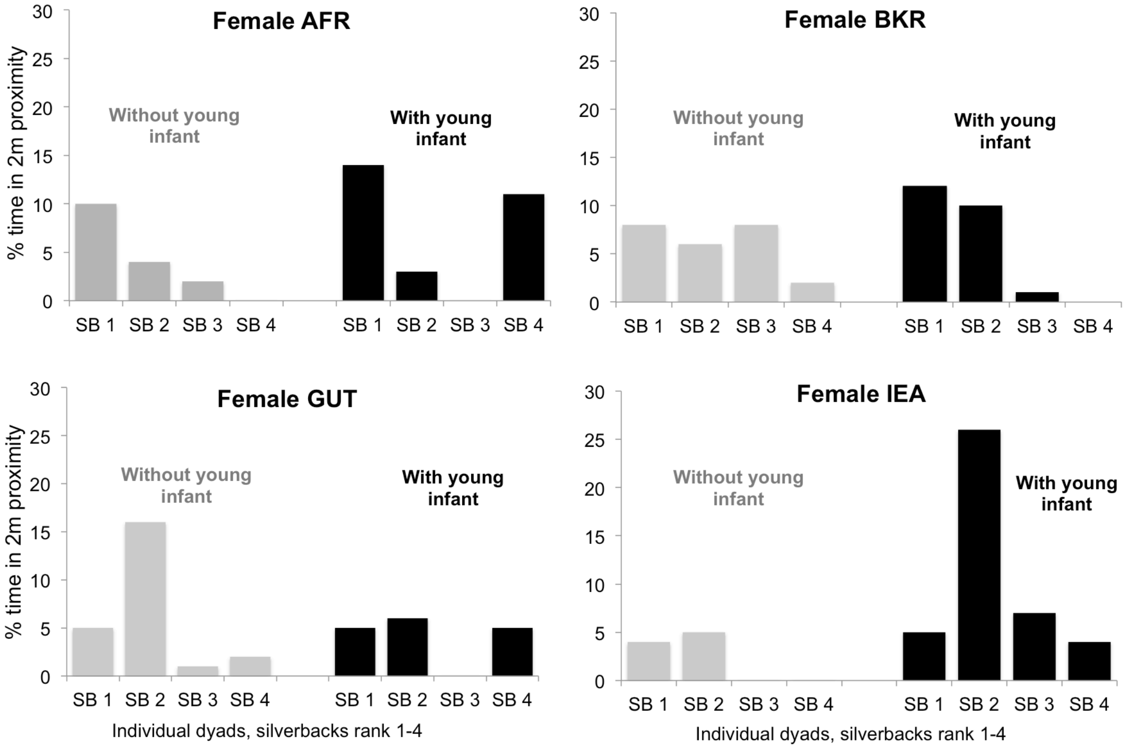

Figure 3.4 Four representative example distributions for amount of time individual females in multi-male groups spent with each available silverback when they had young infants and when they did not.

Prediction 4: Females' top silverback social partner will be the same silverback social partner infants prefer when they are two years old.

We were able to evaluate this prediction for 18 infants. In 16 of 18 cases (89%), the silverback that a mother spent the most time with during her infant's first year of life was also the male that her infant spent the most time with when they were two years old. In one of these 16 instances the mother had two equally preferred partners, and the infant's most preferred partner was one of these two males. In two other cases, there was a mismatch between the mother's top partner and her infant's top partner. For one pair, the female's partner choice outranked the infant's; in the other, the infant's choice outranked the female's (Table 3.5).

Table 3.5

Rank of mother #1 male social partner	**Rank of infant genetic father**	**Rank of infant #1 male social partner @ 24-36 mo.**	**Do mother and infant prefer same male partner?**	**Does mother most prefer infant's genetic father?**	**Does infant most prefer genetic father?**
1	1	1	Yes	Yes	Yes
1	1	1	Yes	Yes	Yes
1	3	Infant died	N/A	No	N/A
1	2	1	Yes	No	No
1	1	1	Yes	Yes	Yes
1	1	1	Yes	Yes	Yes
1	Unk (Extra-group)	1	Yes	N/A	N/A
1	1	1	Yes	Yes	Yes
1	4 (Extra-group)	1	Yes	N/A	N/A
1	1	1	Yes	Yes	Yes
1	1	2	No	Yes	No
1 & 2 (Tied)	3	1	Yes*	No	No
2**	3	1**	Yes	No	No
2	2	2	Yes	Yes	Yes
2	Blackback	2	Yes	No	No
2	3	1	No	No	No
2	1	2	Yes	No	No
2	Unk	2	Yes	Unk	Unk
2	1	2	Yes	No	No
			89% agreement	50% agreement	47% agreement

*Mother spent 7% of time in 2m proximity to each of the top two ranking silverbacks; infant spent 8% of time in proximity to dominant silverback and 0% to beta silverback; **Silverback was beta ranked when infant was conceived and born, dominant when infant was 24-36 months.

Table 3.5 Mothers' most preferred silverback social partner predicted infants' most preferred silverback social partner preference 89% of the time. Both mother and infant social preferences matched genetic paternity only half the time.

How do females with young infants choose silverback partners?

In all 19 cases evaluated, the females' top social partner (measured as time spent in 2m proximity) was the 1st or 2nd ranking male in the group (Table 3.5). In 50% of the 16 cases where paternity was available and the father resided in the group, the female's top partner was also the infant's father. In the remaining cases, there was a discrepancy between the identity of the mothers' top partner and the identity of the sire.

We compared four models to determine whether male rank, paternity, or an interaction between the two best predicted how much time females spent in close proximity to males when they had new infants. The model containing only male rank as a predictor variable had the best (lowest) AICc score (Table 3.6); females spent far more time near males of high rank than near males of low rank.

Table 3.6 (All dyads in multi-male groups)

% time in 2m proximity	**Coef.**	**Std. Err.**	**Z**	**P>|z|**	**95% CI (lower)**	**95% CI (upper)**	**n (dyads)**
Male rank	-0.026	0.007	-3.93	0.000	-0.039	-0.013	α=12, β=10 γ=10, δ=11
Constant	0.107	0.018	5.90	0.000	0.072	0.143	
AICc=-123.10							
Paternity	-0.003	0.016	-0.18	0.854	-0.035	0.029	Father=10 Not father=33
Constant	0.042	0.012	3.48	0.000	0.018	0.066	
AICc=-116.97							
Male rank	-0.029	0.007	-4.33	0.000	-0.041	-0.016	α=12, β=10 γ=10, δ=11
Paternity	-0.016	0.016	-0.95	0.342	-0.048	0.017	
Constant	0.117	0.019	6.10	0.000	0.080	0.155	
AICc=-115.55							
Male rank	-0.027	0.007	-3.88	0.000	-0.041	-0.013	α=12, β=10 γ=10, δ=11
Paternity	0.011	0.037	0.31	0.758	-0.062	0.085	Father=10 Not father=33
Rank*Paternity	-0.014	0.017	-0.83	0.407	-0.049	0.020	
Constant	0.113	0.020	5.64	0.000	0.074	0.152	
AICc=-107.96							

Table 3.6 The model containing only silverback dominance rank best predicted how much time females with young infants in multi-male groups spent in close proximity to adult males.

Discussion

These results provide further evidence that male-female associations in gorillas are motivated by infant protection. In single-male groups, the benefits to all three parties are most pronounced. Females who have the highest risk of infanticide losses and males who have the highest paternity certainty affiliate more than any other type of male-female dyad. These types of dyads may have historically also suffered from the highest losses to predation. While females have little control over the death of an adult male, encouraging close association between her infant and the silverback might make infants less likely to be victims of either leopards or outside males. Encounters with lone silverbacks often begin with the lone male following closely and quietly, perhaps evaluating the risk and potential rewards of engaging with a mixed-sex social unit (pers obs, Karisoke long-term records). In a multi-male group, the presence of non-dominant males—who typically spend more time on the edges of the main social group—make early detection and rebuff much more likely.

In addition to spending more time close to silverbacks, mothers of young infants in single male groups spend more time actively engaged with silverbacks than other types of females do. Grooming and resting in contact provide infants and silverbacks opportunities to interact directly. It is not uncommon to see silverbacks and very young infants reach out to touch each other when new mothers are in physical contact with males. Infants will climb from their mother's bodies onto whatever part of a silverback the female is touching. It is unlikely that these changes in maternal behavior are attributable solely to desire for immediate protection, since this could be achieved simply by remaining nearby. Instead, these early encounters may encourage infants and males to interact and facilitate relationship development. Two-meter proximity is only a body length for this species, much closer than necessary for effective protection from extra-group males. If predation risk also shaped this behavior, then close proximity might have been important because cats attack so quickly.

Intriguingly, few of the behavioral changes observed in single-male groups occurred in multi-male groups, where paternity certainty and risk of infanticide are lower, and predation risk might also have been lower. Females in these groups may be confident their infants are already well protected simply by living with multiple silverbacks, obviating the need for additional measures. Some of our study groups contained large numbers of adult males, and would likely present an insurmountable challenge for even the most determined extra-group male.

We predicted that in these multi-male groups, females with young infants would concentrate their socializing on one male. The opposite was true; they appeared to be using a subtle form of paternity confusion after an infant was born. We can think of no alternative explanation for females' increase in time near the males they spent the least time with when they did not have young infants. Although there were insufficient approach/leave interactions to directly evaluate whether the females or males were primarily responsible for this change, in general females are more responsible for proximity maintenance outside of estrous periods than males are (e.g. Sicotte 1994). Also, since males of lower choice ranking also were generally of lower dominance rank, and there was a trend for females to increase their approaches to such males when they had new infants, it is reasonable to suppose that females are primarily responsible for the result. Even if overall time together is still low, opportunities for “introduction” of all silverbacks to the new infant may help deter intragroup aggression or infanticide, and encourage male participation in defense should it be necessary. Too close an association with one specific partner might actually be dangerous, discouraging other males from offering tolerance and protection.

Even though these females are not directly facilitating male-infant relationships, female social preference is clearly transmitted to infants in multi-male groups. Two years old is the age at which infants spend the most time near silverbacks (Rosenbaum et al. 2011), and during this year time spent near mothers drops sharply (Fletcher 2001). Two year olds are both vulnerable to infanticide and very independently mobile, so their choice of male partner is likely the most important social decision they make. Relying on maternal judgment is an obvious, safe strategy for infants. We found only one case where an infant’s preferred male social partner was lower-ranked (and potentially of lower quality) than his mother’s. This infant had two maternal brothers, 14 and 11 years old, who were often observed near the infant’s preferred male. He may have been preferentially associating with them, and in the process ensured far more protection than he would have staying near his mother’s top social partner.

Females use rank, not paternity, to choose male social partners when their infants are small. While paternity certainly correlates with rank, non-dominant males are siring infants regularly (in this small sample, 47% of infants). It remains unclear whether females can detect paternity. They may be associating with dominant silverbacks more because statistically, they are the most likely fathers; alternatively, they may seek them out because they are higher quality males and therefore better defenders against infanticide. Infants develop a strong social relationship with one male rather than associating equally with all of them. It would be logical to encourage infants to spend time with the highest-quality male even if these social preferences do not match genetic paternity, provided the male is willing to protect the infant. This strategy is dependent on a certain amount of paternity uncertainty to keep all males invested. Female mountain gorillas in multi-male groups regularly mate with multiple males, and we now have evidence they continue cultivating uncertainty after infants are born. Paternal care in mountain gorillas is low-cost whereas losing infants is extremely costly, so males should err toward infant protection. Even minimal effort from a female should be enough to tip the balance.

It is unclear why the females in this sample did not also bias conceptions more heavily toward high-ranking/high-quality males, instead of conceiving with low-ranking males. None of the females were constrained by relatedness; those who conceived with lower-ranking males all had unrelated higher-ranking males available to them. Anecdotally, females may be able to determine future male quality early in a male's life, or recognize potential in males who are queuing behind an aging dominant silverback. The males who have sired multiple infants while exceptionally young or lower ranking have eventually reached dominant status in nearly every case (Karisoke long-term records). Females may want to secure these males' high quality genes, but recruit a current dominant silverback to protect resulting offspring. Human females can employ this dual mating strategy (reviewed in Pillsworth & Haselton 2006), and it appears that at least some of the time, gorilla females might as well.

These data give more insight into the remarkable behavioral flexibility of a species that, at least ostensibly, evolved a single-male/multi-female social system (e.g. Harcourt & Stewart 2007). Females modify their social behavior based on a specific risk associated with group structure. More work is needed to evaluate the long-term outcome of females' social strategies in different group types, and determine what other social behaviors vary with specific structural features.

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Chapter 4

Long-term social partner preferences between adult male and maturing mountain gorillas (*Gorilla beringei beringei*)

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Abstract

Across the animal kingdom long-term social relationships outside the context of pair bonding are rare, but have been demonstrated in some mammals including primates, cetaceans, and social carnivores. The ontogeny of these relationships is likely to depend on the benefits individuals can gain by cultivating such associations. Previous studies demonstrated that young mountain gorillas (*Gorilla beringei beringei*) have strong relationships with adult males, but little is known about the longevity of their associations. Here we examine the temporal stability of proximity relationships between co-resident adult male and maturing gorillas in the habituated population monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center in Volcanoes National Park, Rwanda. Using spatial proximity data, we assessed the strength of adult males' relationships with infants/juveniles, and tracked changes in their relationships as the infants/juveniles matured into subadults (3-4 years later; n=229 dyads) and then became young adults (7 years later; n=42 dyads). The preferences of infants/ juveniles of both sexes were predictive of their preferences as both subadults and young adults, although some young adult males who had lost their preferred partner from juvenilehood developed strong new preferences for males that had risen in the dominance hierarchy. Our data suggest that 1) kin selection may play a more important role in social relationships between possible fathers and adult female offspring than previously suspected, and 2) when maturing males' preferred adult male social partners remain available to them, their relationships can be stable well 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). Animals derive many kinds of benefits from both intra and inter-sex social bonds, depending on the species' ecology and social structure. In socially monogamous species, investment in long-term 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: Matysiokova & Remes 2013; mimic poison frog: Tumulty et al. 2013). For many non-monogamous species, bonds with partners other than mates have important fitness consequences. Social partners provide support that facilitates access to food (chimpanzees: Mitani & Watts 2001), social status (Assamese macaques: Schülke et al., 2010; Berghänel et al., 2011), reproductive opportunities (dolphins: Connor et al. 1992), and social information or support/protection (e.g. lions: Packer & Pusey 1983; coatis: Russell 1983; elephants: McComb et al. 2001; baboons: Silk et al. 2009), all of which may improve fitness outcomes.

The utility of social bonds with particular partners can change over time. Maturation, changes in social or reproductive status, or fluctuating group structure may increase or decrease the value of individuals as social partners. For example, male-female "friendships" in 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 to compete with breeding animals (banded mongoose: Cant et al. 2001). Changes in social partner value 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 the 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 older maternal brothers, but their brothers are likely to disperse when they reach sexual maturity (Engh et al. 2009).

Mountain gorillas (*Gorilla beringei beringei*) provide an important opportunity to investigate the longevity of social bonds 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). Specifically, 60% of females reproduce in their natal group (Robbins et al., 2009a), and 50% of males remain in their natal groups (Stoinski et al. 2009a). Of the male that do disperse, few leave before they are full silverbacks (12-14 years, Watts & Pusey 1993, Stoinski et al. 2009a). Second, tenure of alpha males can be long, up to 19 years (upper life expectancy for the species is ~30-35 for males and 35-40 for females; Bronikowski et al. 2011). These two factors allow us to track social bonds across time, and to investigate possible reasons for changes in the strength of relationships. Silverbacks 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 eventually become rivals or allies for maturing males, or present inbreeding hazards for maturing females.

Because male gorillas often do not disperse, approximately 40% of the gorilla groups in the Virunga massif contain multiple adult males (range: 2-9; Weber & Vedder 1983, Gray et al. 2010). For nine years, the social groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center were exclusively multi-male, and remarkably large. From 2000 to 2007 social group size ranged from 22-64 individuals, with at least four silverbacks in each of the three monitored groups. Our previous work found that the males in these large multi-male groups formed close relationships with immatures (Rosenbaum et al. 2011), but nothing is known about the trajectory of such relationships as young animals mature and social dynamics change. Starting in late 2007, one of these groups split into three, a second split into two, and the third lost almost one third of its females and subordinate males to dispersal (see Caillaud et al. 2014 for demographic details).

The goal of this study is to evaluate the temporal stability of associations between adult male and maturing gorillas in multi-male groups. We noted in an earlier study (Rosenbaum et al. 2011) that immatures of both sexes spend progressively more time with non-dominant males over the first five years of their lives, suggesting that immatures may systematically alter their preferences as they mature. Harcourt & Stewart (1981) observed 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. Stoinski and colleagues (2009a) reported that maternal absence was a predictor of adult male dispersal even though mothers and sons may have long ago severed any obviously beneficial ties. However, the stability of associations between adult male and maturing mountain gorillas has not been systematically evaluated.

Predictions

We predict that the adult male partner preferences of maturing males will be more stable than partner preferences of maturing females for three reasons. First, unlike females, males are unable to transfer between groups. Thus, the primary path for a male to reside in a multi-male group is to remain in his natal group (Robbins 1995). Since multi-male groups may offer benefits, maturing and fully adult males could profit from developing and maintaining tolerant relationships with one another. These benefits include increased rates of infant survival and female retention (e.g. Watts 1989, Sicotte 1993, Robbins 1995, but see also Robbins et al. 2013) and potential for queuing for dominance (Robbins & Robbins 2005) and its associated reproductive benefits. 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 as an inbreeding avoidance measure. Additionally, long-term relationships between males and females are rare in adult animals outside the context of mating.

Methods

Subjects and data collection

This study uses 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 instantaneous sampling of proximity for all animals over one year of age. Every ten minutes, researchers record the identity of all animals within a 2-meter radius of the focal animal. Data were collected by a variety of observers who passed repeated inter-observer reliability tests. Data analyzed here were collected in 2004, 2007, and 2011. The sample includes all adult male and maturing gorillas living in the habituated KRC population who were 1) co-resident in a social group for at least two of the three analyzed years, and 2) co-resident for at least 5 months in each of the years the dyad was analyzed. The sample consists of 229 dyads, involving 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 one to five years; by the end, the oldest were 12 years of age.

During the seven year time span considered here there was significant social upheaval in the study groups, including 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 three-year absence; and group fissions that eventually split three social groups into nine. Figure 4.1 summarizes changes in group composition across time for the animals included in these analyses; changes in group name represent group fissions. The number of dyads decreases across time as subjects died, dispersed, or were separated during group splits. See Caillaud et al. (2014) for complete demographic details across KRC's monitored gorillas.

Measure of social preference

To measure social preference, we used information about close (<2 meter) proximity patterns. For gorillas, time spent in close proximity is an important measure of social closeness and has been used in many previous studies of both wild and captive animals (e.g. Watts 1992 & 1994; Nakamichi & Kato 2001, Stoinski et al. 2003). Maternal relatives and longer-term social partners (i.e., natal residents versus immigrants) spend more time in proximity to one another than unrelated or new social partners (Watts 1992 & 1994). Avoidance of close proximity may be used to deter aggression, particularly for males (e.g. Robbins 1996), and initiating/maintaining close proximity is a primary post-conflict reconciliation mechanism (Mallavarapu et al. 2006). Moreover, proximity is less likely to be strongly influenced by the developmental stage or sex of the maturing partner than other behavioral measures, such as play and grooming which change with age (Meder 1990, Maestripieri & Ross 2004, Rosenbaum et al. 2011). This is important since we are evaluating the long-term progression of social relationships across maturing animals' developmental stages. Across species, proximity is generally correlated with other measures of affiliation (e.g. baboons: Silk et al. 2003; mandrills: Charpentier et al. 2007; 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). Finally, proximity tolerance can be a proximate mechanism underlying fitness benefits (sea lions: Wolf & Trillmich 2008; Columbian ground squirrels: Viblanc et al. 2010).

Categorization of age/sex classes

Our analyses are based on data collected during three time periods: 2004, 2007, and 2011. Males that were at least 8 years of age in 2004 were classified as adults. Although males do not reach full adulthood until they are 12-14 years of age (Watts &

Pusey 1993), they begin exhibiting some forms of adult behavior, including copulations, by the age of eight (Robbins 1995).

During each time period, we categorized maturing partners into three developmental categories: juveniles, subadults, and young adults. Individuals that were 1-5 years old in 2004 were categorized as juveniles in the first time period, then as subadults during the second time period, and as young adults in the third time period. Similarly, animals that were 1-5 years old during the second time period were categorized as juveniles during that time period, and as subadults in the second time period (Figure 4.1).

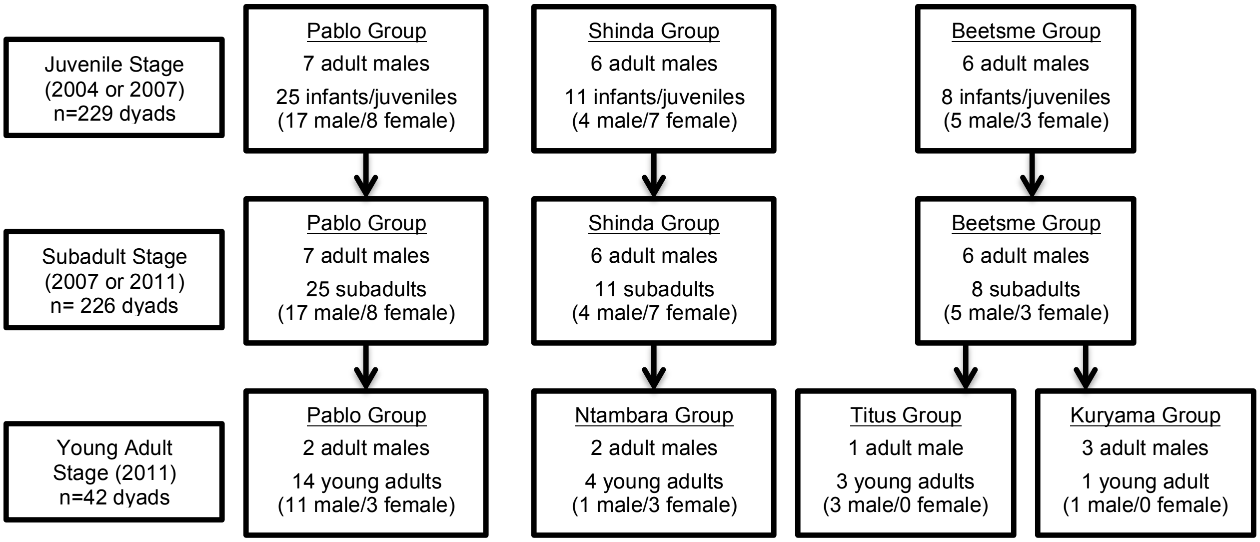

Fig 4.1 Samples sizes and progression of group composition at the three developmental stages for maturing gorillas.

Dominance rank

Adult males were assigned ranks based on non-aggressive 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 the third time period. This change in rank 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 relationships of all natal individuals were known. Thirteen dyads were composed of maternal siblings (n=4 male/male dyads, 9 male/female dyads). All of the sibling dyads were observed in the juvenile and subadult stages; only two dyads were still present during the young adult stage. Sibling and non-sibling dyads have similar age differences (random effects ANOVA: β=1.88, SE=2.17, Z=0.87, P=0.39), and spent similar amounts of time together across all developmental stages (siblings: 5.1%, SD=3.4%; non-siblings: 4.7%, SD=5.5%).

For one analysis we divided males into probable and unlikely fathers. We categorized males as probable fathers if they were at least 14 years older than the maturing partners of the dyad(s) in question. Males do not reach full size until they are ~14 years old. Since these males are probably better competitors and higher in the dominance hierarchy than smaller, younger males, they are more likely than younger males to be the sires of infants. For one dyad classified as probable father/daughter, the adult male was also the female's maternal brother.

Data summary and statistical tests

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

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 (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 males that held the three highest ranks.

The unit of analysis was the dyad. To assess factors related to proximity, we used multi-level, 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 these models to test whether social partner preference at one developmental stage predicted social partner preference at subsequent developmental stage(s). The sample size varied across analyses as animals moved in and out of the sample due to death, dispersal, and specific requirements for analyses. In two cases we used the difference of adjusted Akaike Information Criteria (ΔAICc) values to determine which model(s) best fit the data (Anderson & Burnham 2002). All data analysis was done using Stata 13.

Results

Preferences of infant/juveniles

As in previous studies, juveniles spent substantially more time in proximity to higher-ranking than lower-ranking males (Table 4.1a). When we restricted the analysis to dyads including the three highest-ranking males, the same pattern holds (Table 4.1b). Juvenile sex had no effect on proximity to adult males.

Table 4.1a *(All dyads, n=229)*

Juvenile stage	Coef.	Std. Err.	Z	P>|z|	95% CI (lower)	95% CI (upper)
Rank	-0.033	0.004	-8.60	0.000	-0.040	-0.040
Sex	0.003	0.006	0.41	0.680	-0.010	0.015
Constant	0.149	0.013	11.26	0.000	0.123	0.175

Table 4.1b *(Top 3 ranked males, n=80)*

Juvenile stage	Coef.	Std. Err.	Z	P>|z|	95% CI (lower)	95% CI (upper)
Rank	-0.050	0.016	-3.12	0.002	-0.082	-0.019
Sex	0.007	0.017	0.44	0.659	-0.026	0.041
Constant	0.173	0.030	5.83	0.000	0.115	0.231

Table 4.1a & b: At the juvenile stage, dyads that included higher-ranking males spent more time together than dyads containing lower-ranking males. Sex of the immature did not predict time spent with male partners.

Preferences of subadults

The social preferences of juveniles predicted their preferences as subadults (Table 4.2a). Juveniles that spent a large percentage of time near a particular male continued to spend a lot of time near the same male as subadults. Like juveniles, subadult gorillas of both sexes maintained a clear preference for high-ranking adult males. Subadult males spent more time in proximity to adult males of all ranks than did subadult females, but this difference disappeared when the analysis was restricted to dyads including the three top-ranking males (Table 4.2b).

Visual examination of the data revealed a possible interaction between juveniles' preferences and their sex, so we added an interaction term to the model (Table 4.2c). Juvenile preference predicted the subadult preferences of both sexes, but this pattern tended to be stronger for males than for females (simple slope for males: 0.614; for females, 0.419 p=0.073; Figure 4.2). AIC scores for models with and without the interaction term are very similar, with an ΔAIC of 1.43.

Table 4.2a *(All dyads, n=226)*

Subadult stage	**Coef.**	**Std. Err.**	**Z**	**P>|z|**	**95% CI (lower)**	**95% CI (upper)**
Juvenile stage	0.516	0.072	7.18	0.000	0.375	0.657
Rank	-0.016	0.005	-3.15	0.002	-0.026	-0.006
Sex	-0.022	0.010	-2.14	0.033	-0.041	0.002
Constant	0.087	0.019	4.72	0.000	0.051	0.124

Table 4.2b *(Top 3 ranked male only, n=99)*

Subadult stage	**Coef.**	**Std. Err.**	**Z**	**P>|z|**	**95% CI (lower)**	**95% CI (upper)**
Juvenile stage	0.496	0.087	5.68	0.000	0.325	0.667
Rank	-0.050	0.016	-3.12	0.002	-0.081	-0.019
Sex	-0.025	0.015	-1.61	0.107	-0.055	0.005
Constant	0.142	0.035	4.07	0.000	0.074	0.211

Table 4.2c (*All dyads, n=226*)

Subadult stage	**Coef.**	**Std. Err.**	**Z**	**P>|z|**	**95% CI (lower)**	**95% CI (upper)**
Juvenile stage	0.614	0.090	6.85	0.000	0.438	0.789
Rank	-0.015	0.005	-3.03	0.002	-0.025	-0.005
Sex	-0.011	0.012	-0.98	0.328	-0.034	0.011
Sex*Juv Stage	-0.195	0.109	-1.79	0.073	-0.409	0.018
Constant	0.080	0.019	4.33	0.000	0.044	0.117

Table 4.2a: At the subadult stage, dyads containing high-ranking males and dyads that spent the most time together in the juvenile stage spent more time in close proximity; male/male dyads also spent more time in close proximity than male/female **(4.2b)** When only dyads including the top three ranking males are included, male/male and male/female dyads spent the same amount of time together; (**4.2c**) Juvenile stage preference predicted subadult stage preference more strongly for male/male dyads than male/female (p<0.1).

Figure 4.2

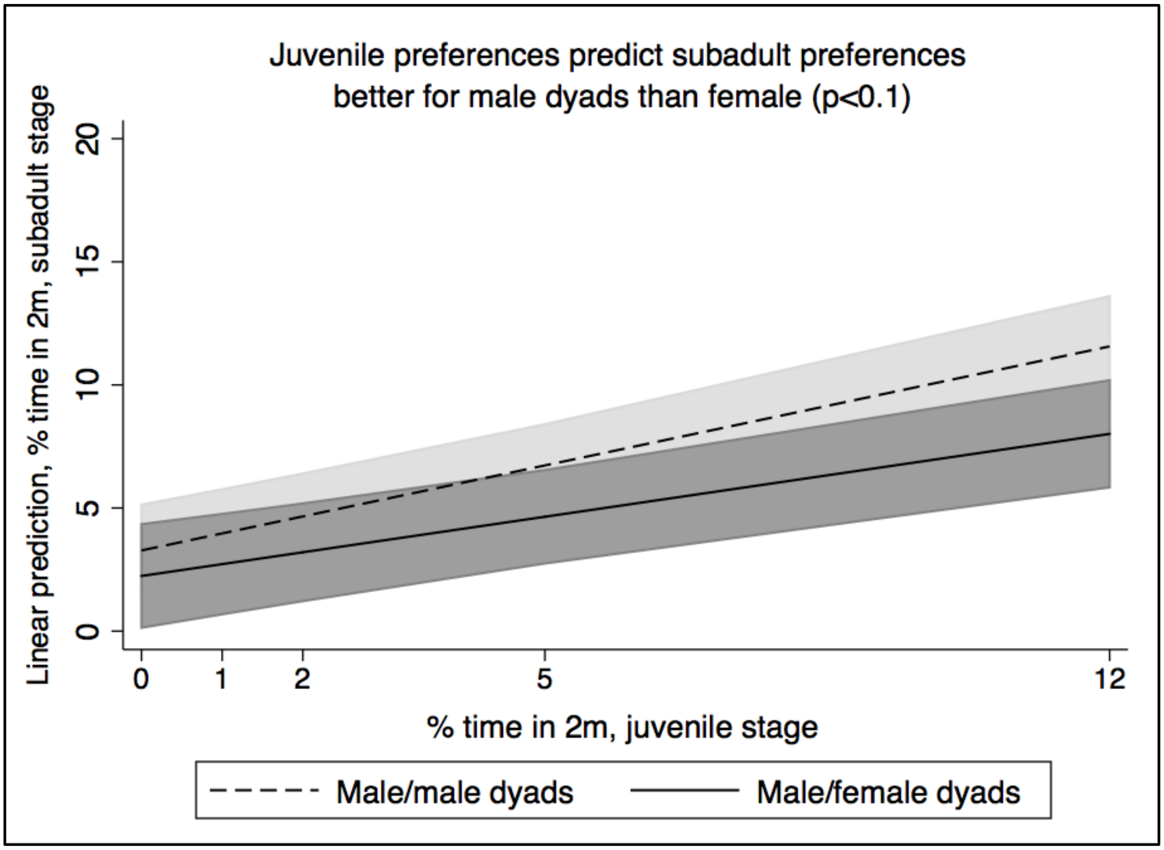

Fig 4.2 Juvenile preference predicted subadult preference better for male/male dyads than male/female dyads ($p<0.1$). Plot of the conditional marginals, with x-axis ticks representing the 10th, 25th, 50th, 75th, and 90th percentiles of time in close proximity values for all dyads in the juvenile stage. Shaded areas are 95% confidence intervals for prediction lines.

Preferences of young adults

By the young adult stage, 22 maturing animals remained who still resided with at least one adult male they had lived with as a juvenile. Eleven maturing animals (eight males and three females) no longer had the adult male partner they had spent the most time with as juveniles available to them (hereafter referred to as their "preferred male"). All previously subordinate adult males had either moved up in their group's dominance hierarchy or dispersed by this point, so every remaining adult male partner now held one of the top three dominance ranks.

Visual examination suggested that the distributions of time spent with adult male partners in the young adult stage were different for animals that did and did not have their preferred partner from the juvenile stage present (Figure 4.3). Specifically, it appeared that young adults whose preferred juvenile stage partner was no longer available were now spending more time with a male they had previously spent little time with, rather than forgoing spending time in close proximity to an adult male. The increased time with these partners meant there was no difference in the mean amount of time maturing animals who did and did not have their earlier preferred partner available spent with adult male social partners overall (juvenile preferred partner present: mean=0.04, SD=0.04, min=0.00, max=0.13, n=23 dyads; juvenile preferred partner absent: mean=0.06, SD=0.05, min=0.00, max=0.16, n=19 dyads; z=0.35, p=0.727).

Figure 4.3

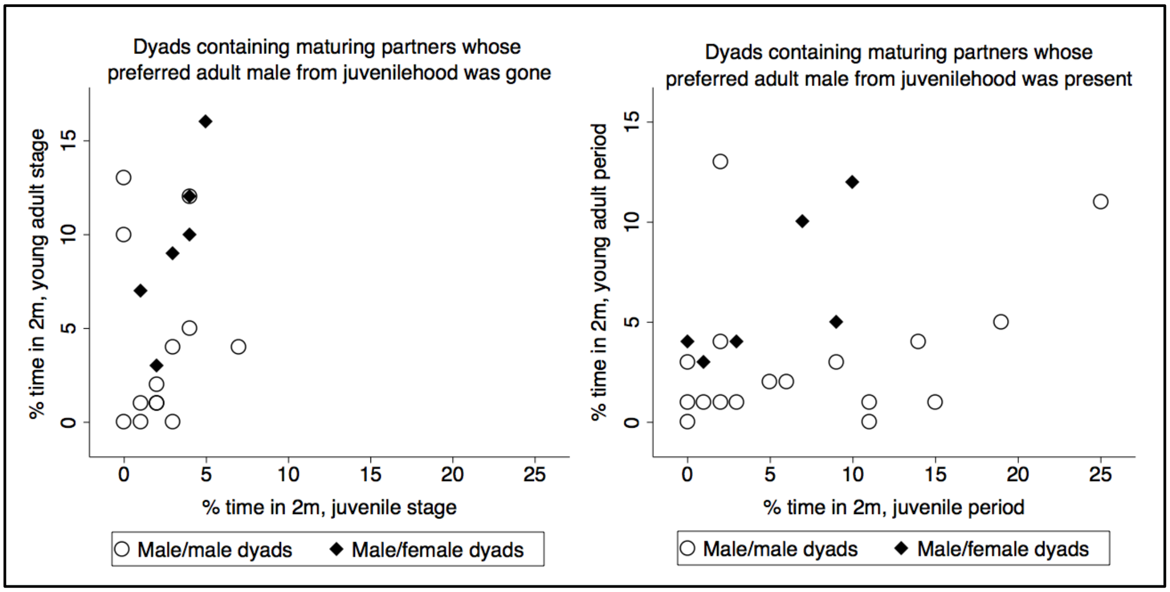

Fig 4.3 Visually, young adult animals that lost their most preferred male partner from the juvenile stage appeared to increase their time near male partners they had spent little time with previously, rather than forgoing time near male partners. For maturing animals who still had their most preferred partner from the juvenile stage available, juvenile stage preferences appeared to predict young adult stage preferences.

Visual examination also suggested there was once again an interaction between sex and earlier preference. The number of male/female dyads was small (n=12), but there were no remarkable outliers. Females' juvenile stage preferences visually matched their young adult preferences very well (Figure 4.4). Females who had lost their preferred partner increased their time near a new male, but the new partner appeared to be predicted by their juvenile preference; they did not change to males they had no relationship with as juveniles. Females who had their most preferred juvenile stage partner available spent the same amount of time with male partners overall as females who had lost their most preferred juvenile stage partner (juvenile preferred partner present: mean=0.06, SD=0.04, min=0.03, max=0.12, n=6 dyads; juvenile preferred partner absent: mean=0.10, SD=0.04, min=0.03, max=0.16; z=0.80, p=0.424).

For male/male dyads, four notable outliers spent much more time together in the young adult stage than the juvenile stage might predict (Figure 4.4). Three of these young adult partners had lost their preferred male from juvenilehood, but one had not. All four dyads contained former subordinate males who were now alpha (three males) or beta (one male) rank. Like females, males who did and did not have their preferred partner available from the juvenile stage spent the same amount of time near adult males (males with preferred partners: mean=0.03, SD=0.04, min=0.00, max-0.13, n=17 dyads; for males without preferred partners: mean=0.04, SD=0.05, min=0.00, max=0.13; z=0.13, p=0.898). Unlike the maturing females, however, the males they ‘switched’ to were not predicted by their juvenile preference.

Figure 4.4

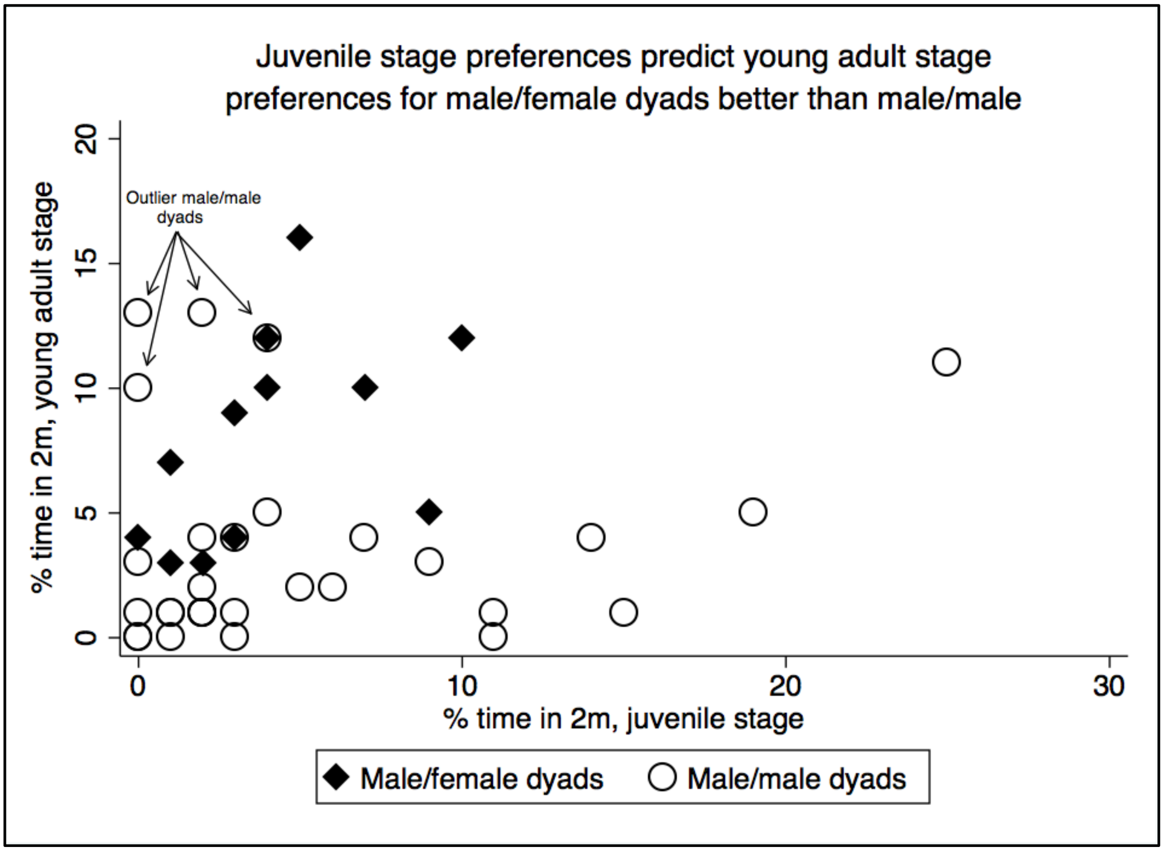

Fig 4.4 Juvenile preference predicted young adult preference for male/female dyads better than male/male, but this was highly influenced by four outlier male/male dyads. Three of the maturing males had lost their preferred juvenile stage adult male; the fourth now spent equal time with his previously preferred adult male and the new dominant male. For females, juvenile stage preferences were highly predictive of young adult stage preferences even if they had lost the partner they originally spent the most time with. Unlike for male/male dyads, their juvenile stage preferences predicted which males they would 'switch' to.

We tested two models that contained all 42 dyads. The first model contained four main effects predictors: male rank, presence of preferred partner from juvenilehood, preference in the juvenile stage, and sex. Male/female dyads spent more time together in the young adult stage than male/male dyads did (Table 4.3a). The other three variables did not predict time spent together in the young adult stage.

The second model contained an interaction term for sex and juvenile preference. Male/female dyads' time spent together in this stage was predicted by juvenile preference, but the same was not true of male/male dyads (Table 4.3b). The model containing the interaction term was a better fit (i.e., had a lower AIC). The model with only main effects had an ΔAIC of 3.69.

Finally, we ran the interaction model again with the four outlier male/male dyads removed. Without these dyads, preference in the juvenile stage predicted preference in the young adult stage (Table 4.3c).

Table 4.3a *(All males (no subordinate males remaining, n=42))*

Young adult stage	Coef.	Std. Err.	Z	P>|z|	95% CI (lower)	95% CI (upper)
Juvenile stage	0.183	0.135	1.35	0.176	-0.082	0.448
Rank	-0.017	0.023	-0.76	0.448	-0.062	0.027
Sex	0.036	0.015	2.50	0.012	0.008	0.065
Juv pref partner present	-0.007	0.016	-0.46	0.648	-0.038	0.024
Constant	0.075	0.037	2.01	0.045	0.002	0.148

Table 4.3b *(All males (no subordinate males remaining, n=42))*

Young adult stage	Coef.	Std. Err.	Z	P>|z|	95% CI (lower)	95% CI (upper)
Juvenile stage	0.144	0.130	1.11	0.268	-0.111	0.398
Rank	-0.012	0.024	-0.50	0.615	-0.059	0.035
Sex	0.002	0.018	0.12	0.901	-0.034	0.038
Juv pref partner present	-0.007	0.015	-0.48	0.634	-0.035	0.022
Sex*juv stage	0.757	0.285	2.66	0.008	0.199	1.316
Constant	0.073	0.040	1.81	0.070	-0.006	0.151

Table 4.3c *(Outlier dyads removed (no subordinate males remaining, n=38))*

Young adult stage	Coef.	Std. Err.	Z	P>|z|	95% CI (lower)	95% CI (upper)
Juvenile stage	0.236	0.095	2.49	0.013	0.050	0.422
Rank	0.007	0.015	0.45	0.652	-0.023	0.037
Sex	0.022	0.014	1.59	0.113	-0.005	0.048
Juv pref partner present	-0.008	0.010	-0.81	0.419	-0.029	0.012
Sex*juv stage	0.651	0.221	2.95	0.003	0.219	1.084
Constant	0.017	0.026	0.63	0.527	-0.035	0.068

Table 4.3a: In the young adult stage, male/female dyads spent more time in close proximity than male/male dyads; **(4.3b)** When all dyads are included, juvenile stage preference predicted young adult stage preference for male/female dyads but not male/male; **(4.3c)** Juvenile preference predicted young adult preference for both sexes if four outlier male/male dyads are removed, but juvenile preference still predicted young adult preference more strongly for male/female dyads than male/male.

Last, we evaluated whether young adult females changed the amount of time they spent in 2m proximity to males that were old enough to be their probable fathers compared to males closer to them in age. Of the 12 total dyads, seven were <14 years apart in age and therefore categorized as unlikely father/daughter dyads. All seven of these dyads spent more time together when the maturing female was a young adult than they had when she was a juvenile (mean change in time=+4.0%, SD=2.8%). The remaining five dyads were probable father/daughter dyads. Four spent more time together when the female was a young adult than when she was a juvenile; the fifth decreased its time together (mean change in time=3.6%, SD=5.5%). Thus, there is no indication that females are systematically avoiding males that are old enough to be probable fathers.

Discussion

Our data confirm results from previous studies which indicate that young gorillas have strong preferences for high ranking adult males (Fossey 1979, Stewart 2001, Rosenbaum et al. 2011), and extend previous findings to demonstrate that gorillas maintain these preferences as they mature into subadults and then (at least for females) become young adults. These data raise two related questions: first, why are juvenile gorillas attracted to high-ranking males, and second, what benefits do young gorillas gain from maintaining these relationships as they mature?

Why dominant males?

Male dominance in this species, like many others, is correlated with reproductive success (Bradley et al. 2005; reviewed in Ellis 1995). It is probable that juvenile gorillas are attracted to dominant males because they are their most likely fathers. However, dominant males are also usually the highest-quality males in multi-male groups. The primary benefit adult males offer to juveniles is protection against infanticide. Even if a dominant male is not a juvenile's father, if he is the highest-quality male available and is willing to provide protection, juveniles might prefer the dominant male to a lesser-quality father.

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; fjord-living 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). Folivorous mountain gorillas live in a particularly favorable environment. Differential access to food appears to have little effect on life history decisions like dispersal, or on reproductive success (e.g. Robbins et al. 2007, Robbins et al. 2009b). Therefore, it seems unlikely that ecological conditions provide a good explanation for these long-term preferences. It is much more likely that long-term relationships start as a form of parental care or investment, since maturing gorillas are most strongly drawn to high-ranking males who are also their most likely fathers (Bradley et al. 2005).

Once the juvenile stage is over tolerant older males offer other benefits, which are different for male and female maturing partners. Association with top-ranked males has multiple advantages for maturing males. It provides closer proximity to adult females, who tend to congregate around the top-ranked male. It may also help them cultivate relationships with the dominant male himself, which could diminish the likelihood of aggression as they become big enough to be serious competitors. Finally, it may help set young males up to queue behind these older, higher-ranking animals for reproductive access (Robbins & Robbins 2005). Previous work on this population indicates that high-ranking males may need to offer younger/subordinate males breeding concessions to retain them as group members (Stoinski et al. 2009b). Although younger males take breeding opportunities from dominant males, the benefits appear to outweigh the costs as multi-male 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 are expected to have lower lifetime fitness than philopatric males (Robbins & Robbins 2005). Therefore, the inclusive fitness benefits of offering breeding opportunities to potential sons may more than offset occasional lost breeding opportunities for older males. More work is needed to determine who receives concessions and how younger animals' behavior can influence it.

Female gorillas, like most female mammals, are not limited by access to male reproductive partners; their associations with older males are unlikely to directly increase their reproductive output. However, female choice of male social partner is important since males help ensure infant survival. Robbins (2001) found that social patterns during the three years preceding a group split predicted which adult male adult females chose to join (but see also Watts 2003). The current work suggests that preferences can go back much further, and extend beyond favorable breeding partners. Female preferences as juveniles strongly predict their preferences when they are young adults. The magnitude of the slope for females is very high despite the small sample of immature females who remained in the sample as young adults. Half of the young adult females in our sample resided with males who had drastically changed rank and split into new groups. In spite of this, not a single female dyad markedly deviated from this pattern. Their juvenile stage social preference predicted which male they would 'switch' to when they lost their most preferred male. They may feel safest with these males, who have protected them since birth. Even if they are not preferred mating partners because of inbreeding avoidance, they can still provide benefits during resting bouts, feeding, and traveling. All 12 adult male/young adult female dyads occurred in multi-male groups, in which females had other mating options. More work is needed to determine whether such dyads mate and reproduce together, or whether life-long association suppresses mating behavior as is the case for many other primate species (e.g. Paul & Kuester 2004, Muniz et al., 2006).

Adult males might benefit from nonsexual relationships with females as well. Female preference is considered an important component of male mating success in mountain gorillas (Fossey 1982, Watts 1991, discussed in Harcourt & Stewart 2007). Having female followers may help males maintain or elevate their dominance rank. The presence of these females may encourage young males to remain in the group, and this in turn can help groups to retain females (Robbins et al. 2013). Strong bonds between fathers and their adult daughters may allow males to protect their grandchildren from infanticide and predation, primary functions of male-female relationships in gorillas (Harcourt & Stewart 2007).

We predicted that maturing male/adult male dyads would be more stable across time than maturing female/adult male dyads. This prediction was partially supported by the data. The preferences of both male and female juveniles for top-ranking male partners were sustained as they matured into subadulthood. However, when the analysis is extended to include all males, rather than just the top three, there is some evidence that male preferences are more stable than female preferences. Such sex differences could arise because juvenile males are settling on favored low-ranking male partners earlier than juvenile females, or because females are exploring a greater variety of social relationships with males during subadulthood. This is the age at which females first become sexually receptive, and it may be beneficial to extend their social networks to a larger set of males before making decisions about whether to remain in their natal group or transfer to a new group.

Four maturing males in our sample, three of whom had lost their most preferred partner from juvenilehood, developed strong new preferences for males they had spent either no or very little time with as juveniles. The disappearance of an animal's most preferred male social partner from juvenilehood would not necessarily have to result in "replacement;" these young adult males are far past the stage of needing protection.

Instead of choosing to forgo a close adult male social partner, these males instead settled on new partners they had spent little or no time near when they were juveniles. One male changed his top social partner in spite of having his preferred male from juvenilehood available to him, but his was an isolated case. He also did not stop spending time with his old partner. Instead, he spent nearly equal time with both the old and new preferred partners. All four of these new preferred adult male social partners were animals who had risen sharply in rank during the study period. One had been a 3rd ranked male in 2004, and was the top-ranked male in his group in 2011. Two others were subordinates 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 young. After they became high ranking, their value probably increased.

It is important to note that for the other 26 male/male dyads, partner preference in juvenilehood was predictive of partner preference in young adulthood despite fading quality of aging male partners. By 2011, two adult males who accounted for 12 male/male dyads were 25 and 33 years old, and both had younger males in their groups who were almost certainly better competitors. Rather than changing their preferences to mirror these social dynamics, all young adult males save the one mentioned above continued to spend time near the male they had preferred seven years earlier.

These data add to our understanding of gorilla socioecology in two important ways. First, enduring associations between maturing female gorillas and adult males, who in some cases are their fathers but likely not their mates, suggest that kin selection may shape male-female relationships in gorillas to a greater extent than previously suspected. There are few primate species in which females live in groups alongside males that are likely to be their fathers, and there is no previous evidence of lasting ties between males and their adult daughters. Stoinski and colleagues (2009a) found that maternal death or dispersal predicted adult male dispersal, providing intriguing evidence that mother-son relationships maintain importance well into adulthood; these new data imply father-daughter relationships may as well. This suggests an important relationship between adult children and parents, which appear to be almost non-existent outside of the great apes (including humans) unless one sex experiences reproductive suppression (e.g. *Callitrichids*: French 1997; long-tailed tits: Hatchwell et al. 2001; yellow-bellied marmots: Armitage et al. 2011; mole-rats: Lutermann et al. 2013).

Second, our data indicate that young adult males maintain stable and enduring preferences for adult male partners who remain available to them, but can develop preferences for newly dominant males if demographic shifts require it. Notably, there is little evidence here to suggest that male gorillas shift social allegiances in response to changing group dynamics as is commonly observed in male chimpanzees (e.g. de Waal 1982 & 1984; Nishida & Hosaka 1996; Mitani et al. 2000; Duffy et al. 2007), even though male gorillas might ostensibly gain from it. More work is needed to determine whether young males gain long-term fitness advantages from associating with top-ranking males, and whether these relationships are cultivated by young males or their adult male partners.

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