



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



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

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Kin discrimination is useful when social structure facilitates cooperative behaviour (Hamilton, 1964) or enables deleterious inbreeding (Blouin & Blouin, 1988; Lehmann & Perrin, 2003). Accordingly, selection pressure should favour kin discrimination in systems in which costs of misidentification are high, or when the benefits of cooperation are particularly valuable. Examples include socially monogamous species in which one partner may be cuckolded (e.g. New World primates: Achenbach & Snowdon,

2002; Mendoza & Mason, 1986; Tardif, Carson, & Gangaware, 1990; rodents: Cantoni & Brown, 1997; Jones & Wynne-Edwards, 2000; Silva, Vieira, & Izar, 2008; Wynne-Edwards, 1987; birds: Wan, Chang, & Yin, 2013; Webster, Tarvin, Tuttle, & Pruett-Jones, 2007; reviewed in Cockburn, 2006; fish: Balshine-Earn & Earn, 1997; DeWoody, Fletcher, Wilkins, & Avise, 2000; Itzkowitz et al., 2001) or species that rely heavily on cooperative behaviour for mating access, offspring rearing, territory control or food acquisition (e.g. social insects: reviewed in Beshers & Fewell, 2001; Old World primates: Mitani, Merriwether, & Zhang, 2000; Muller & Mitani, 2005, reviewed in Silk, 2002; social carnivores: de Villiers, Richardson, & van Jaarsveld, 2003; Mosser &

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

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

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

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

paternal kin discrimination appears include affiliative behaviour, mate choice and protection against infanticide.

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

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

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

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

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