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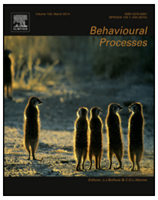

Familiarity is more important than phenotypic similarity in shaping social relationships in a facultative female dispersed primate, *Colobus vellerosus*

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ABSTRACT

Animals often bias affiliative behaviors toward kin, but it is unclear what mechanism most species use to discriminate kin. We investigated if facultative dispersed female primates use phenotype matching and/or familiarity to discriminate female kin. We studied 38 adult female *Colobus vellerosus* at Boabeng-Fiema, Ghana. We determined dyadic co-residency status and age proximity using long-term demographic data, *R*-values from 17 short tandem repeat loci, and interaction rates using focal samples collected during one year. Approach rates were not strongly affected by how long females had resided together, which contrasts to the familiarity hypothesis. Females approached and groomed maternal kin more than other females, which supports the mother-mediated familiarity hypothesis. Females did not discriminate paternal half siblings from non-kin, and they did not prefer to interact with females of similar age. Short-term co-resident kin did not bias affiliation toward each other, indicating that female colobus cannot consistently recognize less familiar kin via phenotype matching or that biasing behaviors toward less familiar kin is not beneficial. Despite showing facultative dispersal that may reduce the accuracy of using familiarity as a kin recognition mechanism, female choice of social partners was based on familiarity, which conforms to the pattern observed in many female philopatric primates.

1. Introduction

Animals bias affiliative and cooperative behaviors toward kin in a wide range of animals (Archie et al., 2006; Gompper et al., 1997; Griffin and West, 2003; Guilhem et al., 2000; Hirsch et al., 2012; Kapsalis, 2004; Wahaj et al., 2004; Wilkinson, 1986). Despite the widespread presence of kin structured social networks in these animals, little is known about the process by which kin preferences develops, and whether or not the process differs between species (Rendall, 2004; Widdig, 2007). In mammals that are female philopatric (Greenwood, 1980), mothers often form long-lasting bonds with their female offspring, and these enduring bonds lead to mother-mediated familiarity among maternal female kin as they cluster around the matriarch (Chapais, 2001; Walters, 1987). As a result, mother-mediated familiarity may be the basis for maternal kin recognition in female philopatric mammals (Rendall, 2004). Paternal kin bias might also arise due to differential familiarity in species with high reproductive skew and short male tenure (Widdig, 2007), which makes it likely that natal animals of similar age are paternal siblings (Altmann, 1979; Altmann et al., 1996). Because immatures often play with others of similar age, this could lead to age-mediated familiarity among paternal siblings (Smith et al., 2003; Widdig, 2007; Widdig et al., 2001). Even in the absence of familiarity, animals may recognize kin by using phenotype matching if phenotypic similarity is correlated with relatedness (Holmes and Sherman, 1982). Phenotypic similarity in body odors (Mateo and Johnston, 2000), vocalizations (McDonald and Wright, 2011), facial features (Dal Martello and Maloney, 2006; Kazem and Widdig, 2013; Vokey et al., 2004), and pigmentation patterns (Hinz et al., 2012) may allow individuals to discriminate between familiar animals of different kinship categories (Wahaj et al., 2004) and to determine their relatedness with animals that they have not previously encountered (Holmes and Sherman, 1982).

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Most studies investigating kin recognition mechanisms have been conducted in the laboratory. Whether or not experimental findings can be generalized to wild animals is uncertain as the social conditions differ markedly from those in natural settings (Hare, 1998). At least in experimental settings, there is convincing evidence that several species of rodents use phenotype matching to recognize unfamiliar kin (*Peromyscus maniculatus*: Dewsbury, 1988; *Mus musculus*: Kareem and Barnard, 1982; *Mesocricetus auratus*: Mateo and Johnston, 2000; *Spermophilus* spp.: Schwagmeyer, 1988). However, the kin bias is often stronger toward familiar kin than unfamiliar kin, which suggests that both familiarity and phenotypic similarity are important in shaping social behaviors and partner choice in rodents (Koenig, 1994; Villavicencio et al., 2009). Experimental studies of primates are fewer, and the findings are more ambiguous. A small number of infant southern pig-tailed macaques (*Macaca nemestrina*) could discriminate kin despite no previous contact (Wu et al., 1980) while attempts to replicate this study with a larger sample size showed social preferences based on familiarity rather than phenotypic similarity (*Papio cynocephalus*: Erhart et al., 1997; *M. nemestrina*: Sackett and Fredrickson, 1987).

Studies conducted in wild animals to address these issues are often inconclusive due to the difficulties of teasing apart the effects of relatedness and familiarity. The exceptions come from species in which young are reared in nests. At the time of emergence from the nest, the young is more familiar with their littermates than other animals regardless of their relatedness, and this familiarity shapes social relationships (Hare, 1998; Wahaj et al., 2004). There is also another opportunity to decouple familiarity and relatedness when the sex that typically remains philopatric exhibits facultative dispersal. Because some animals of one sex disperse while others remain in their natal group, familiarity might not necessarily correspond to relatedness. *Colobus vellerosus* (ursine or white-thighed colobus monkey) is an African Old World monkey that shows facultative female dispersal (Teichroeb et al., 2009; Wikberg et al., 2012), and females may reside with more or less familiar female kin of different ages. Facultative female dispersal may lead to a more variable distribution of kin compared to female philopatric species, which weakens the correlation between familiarity and relatedness. If kin biased female–female social relationships leads to fitness benefits in this species, it might be necessary for females to use phenotype matching to discriminate kin from non-kin to reap these benefits.

We have previously documented that female colobus bias affiliation toward female kin (Wikberg et al., 2014). To gain insights into the possible use of familiarity and phenotype matching to discriminate kin from non-kin, this paper investigates if females discriminate between social partners (i.e. female group members) based on their co-residency status (e.g. long-term versus short-term co-residents), kinship, age-proximity, and phenotypic similarity estimated via *R*-values (i.e. dyadic estimates of relatedness). The familiarity hypothesis is supported if females distinguish between social partners depending on their co-residency status, kinship, and age-proximity (Rendall, 2004; Smith et al., 2003; Widdig, 2007; Widdig et al., 2001). The phenotype matching hypothesis is supported if females distinguish between social partners based on their *R*-values (Dewsbury, 1988; Kareem and Barnard, 1982; Mateo and Johnston, 2000; Schwagmeyer, 1988).

2. Materials and methods

2.1. Behavioral and demographic data collection

This study was conducted at Boabeng-Fiema Monkey Sanctuary (BFMS), which is a 1.92 km^2 dry semi-deciduous forest (Hall and Swaine, 1981) located in central Ghana (7°43′ N and 1°42′W). At BFMS, *C. vellerosus* reside in groups consisting of 9–38 animals (Wong and Sicotte, 2006). Between 2008 and 2009, we recorded social behaviors ad libitum and during 10-min continuous focal samples (Altmann, 1974) of 38 adult (>5 years) females residing in six groups. We have 1614 contact hours and 619 focal hours with a mean of 16 focal hours per female (range: 14–18 h/female).

We used the focal samples to calculate the proportion of time spent giving grooming and the rate of giving approaches to one meter. We standardized the proportion of time spent grooming using the *z*-transformation (Abdi, 2007). The *z*-scores were calculated separately for each female-partner combination using the following formula: $(y - \dot{X})/\mathrm{SE}$. For example, female A's *z*-score with partner B was calculated as the mean of female A's grooming across partners ($\dot{X}$), subtracted from the grooming between A and B (y), and divided by the standard error for female A's grooming across partners (SE). Partners with scores above one were categorized as preferred partners (Lehmann and Boesch, 2009).

Demographic data were collected by ECW and members of PS's research team at least once a month when observers were present at the field site. The groups were observed for different number of years before the start of this study (2000: BS and WW; 2004: DA, OD, and RT; NP: 2007) and the ability to recognize individuals has increased from a few of the group members to all group members between 2004 and 2008. This allowed us to determine co-residency status, partial pedigrees, and age proximity for some of the study animals. We coded whether or not females were long-term or short-term co-residents (i.e. had resided together for at least four years versus less than four years). Females in BS group and OD group resided with both long-term and short-term co-residents, while all females in DA, NP, RT, and WW were long-term co-residents.

We knew the exact or approximate age of 12 females based on the demographic records. For the remaining females, we estimated their age-class based on their physical appearance (e.g. elongated nipples, body size, wrinkles, hair loss, and body posture). Two experienced observers independently estimated the females' ages and only in three cases did the age classification differ by more than two years. In these three cases, we used the mean estimated age. We used the exact or estimated ages to calculate the age differences between females. If their age difference was less than two years, we considered them as belonging to the same age cohort (Smith et al., 2003). Belonging to the same age cohort may be a rough estimate of the likelihood of being paternal half siblings in this population because the average male tenure is two years (Wikberg et al., 2012) and paternity is heavily skewed toward the alpha male (87.5% in one multi-male group; ECW unpublished data). In one multi-male group, 50% of the infants belonging to the same age cohort and 18% of the infants belonging to different age cohorts were paternal half siblings (ECW unpublished data). We only have access to genetic data from one uni-male group during three years of stable male group membership. All infants born in the uni-male group during this time period were paternal half siblings (ECW unpublished data).

2.2. Genotyping and calculating dyadic estimates of relatedness

We collected at least two fecal samples from each study animal for subsequent DNA extraction, genotyping, and analysis of 17 short tandem repeat loci to infer kinship. For details regarding the laboratory methods and protocol see Wikberg and colleagues (2012). We used the software COANCESTRY (Wang, 2011) to compute *R* following a method described by Rollins and colleagues (2012). This software uses seven methods for calculating dyadic estimates of relatedness (*R*), and we investigate which of these methods is most accurate by correlating *R* with actual relatedness (*r*) using dyads with known kinship (Rollins et al., 2012). We used 105 dyads that included all study animals with known parentage, and the