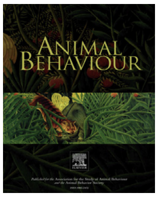
Animal Behaviour 105 (2015) 139–152

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



# Social bonds in the dispersing sex: partner preferences among adult female chimpanzees

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ARTICLE INFO

*Article history:*
Received 2 October 2014
Initial acceptance 23 October 2014
Final acceptance 12 March 2015
Published online
MS. number: A14-00781R2

*Keywords:*
chimpanzee social structure
core area
dyadic association
kin bias
range estimation
social bonding
social preference

In most primate societies, strong and enduring social bonds form preferentially among kin, who benefit from cooperation through direct and indirect fitness gains. Chimpanzees, *Pan troglodytes*, differ from most species by showing consistent female-biased dispersal and strict male philopatry. In most East African populations, females tend to forage alone in small core areas and were long thought to have weak social bonds of little biological significance. Recent work in some populations is challenging this view. However, difficulties remain in quantifying the influence of shared space use on association patterns, and in identifying the drivers of partner preferences and social bonds. Here, we use the largest data set on wild chimpanzee behaviour currently available to assess potential determinants of female association patterns. We quantify pairwise similarities in ranging, dyadic association and grooming for 624 unique dyads over 38 years, including 17 adult female kin dyads. To search for social preferences that could not be explained by spatial overlap alone, we controlled for expected association based on pairwise kernel volume intersections of core areas. We found that association frequencies among females with above-average overlap correlated positively with grooming rates, suggesting that associations reflected social preferences in these dyads. Furthermore, when available, females preferred kin over nonkin partners for association and grooming, and variability was high among nonkin dyads. While variability in association above and below expected values was high, on average, nonkin associated more frequently if they had immature male offspring, while having female offspring had the opposite effect. Dominance rank, an important determinant of reproductive success at Gombe, influenced associations primarily for low-ranking females, who associated preferentially with each other. Our findings support the hypothesis that female chimpanzees form well-differentiated social relationships that are of potential adaptive value to females and their offspring.

Kinship has long been recognized as an important factor mediating the distribution of social interactions among conspecifics, given the inclusive fitness benefits gained by cooperating with relatives (Hamilton, 1964). Empirical evidence from a range of social mammals supports the role of kinship for structuring social relationships within groups (spotted hyaenas, *Crocuta crocuta*: Holekamp et al., 1997; African elephants, *Loxodonta africana*: Archie, Moss, & Alberts, 2006; sperm whales, *Physeter macrocephalus*: Gero, Engelhaupt, & Whitehead, 2008; killer whales, *Orcinus orca*: Pilot, Dahlheim, & Hoelzel, 2010; yellow-bellied marmots, *Marmota flaviventris*: Wey & Blumstein, 2010; Thornicroft's giraffes, *Giraffa camelopardalis thornicrofti*: Bercovitch & Berry, 2013), and this is particularly true for nonhuman primates (reviewed in Langergraber, 2012) and humans (Madsen et al., 2007). Because of sex differences in fitness-optimizing strategies that result in greater resource constraints on reproduction in females than in males, female mammals often benefit most from kin support in resource defence. As a result, mammalian societies with sex-biased dispersal often form around females and their related offspring (Dobson, 1982; Mabry, Shelley, Davis, Blumstein, & Van Vuren, 2013; Pusey, 1987). Thus, it is not surprising that female mammals, more often than males, form the strongest and longest-lasting social bonds, and have evolved hormonal adaptations that facilitate such bonding (Taylor et al., 2000).

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http://dx.doi.org/10.1016/j.anbehav.2015.04.012
0003-3472/

Chimpanzees, *Pan troglodytes*, deviate from the typical mammalian pattern of female philopatry by showing consistent female-biased dispersal and male philopatry (Nishida & Kawanaka, 1972; Pusey, 1979), a feature of social organization shared with their sister taxon, bonobos, *Pan paniscus* (Eriksson et al., 2006; Furuichi, 1989; Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999). Males defend a community range in which females settle, and female eastern chimpanzees, *P. t. schweinfurthii*, in at least two populations establish areas of preferential use within this range, often referred to as “core areas” (Gombe, Tanzania: Murray, Mane, & Pusey, 2007; Williams, Pusey, Carlis, Farm, & Goodall, 2002b; Kanyawara, Kibale National Park, Uganda: Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007; Kahlenberg, Emery Thompson, & Wrangham, 2008b). Within the community range, both males and females freely join or leave subgroups known as “parties” (Goodall, 1986), a characteristic shared with other fission–fusion societies (Grove, 2009; Mann, 2000). As expected based on kin selection theory, male chimpanzees form strong social bonds with other males (Mitani, 2009; Watts, 2002), with measurable effects on rank acquisition and the likelihood of siring offspring (Gilby et al., 2013a).

In most East African populations of chimpanzees, females spend much of their time foraging alone with their dependent offspring (Murray et al., 2007; Wrangham & Smuts, 1980), and it is often assumed that they do so to minimize contest competition over limited resources (Wrangham, 1979). Empirical evidence supports the role of competition in determining female ranging patterns and social interactions. Female core areas vary in resource quality (Emery Thompson et al., 2007; Kahlenberg et al., 2008b; Murray, Eberly, & Pusey, 2006), and higher-ranking females often occupy better habitats (Pusey & Schroepfer-Walker, 2013). Females aggressively defend core areas (Miller et al., 2014), and differences in resource-holding potential may lead to better foraging efficiency among high-ranking females (Emery Thompson et al., 2007; Murray et al., 2006; Williams et al., 2002b), which can influence reproductive success (Emery Thompson et al., 2007; Jones, Wilson, Murray, & Pusey, 2010; Pusey, Williams, & Goodall, 1997).

Given competition over resources and the general absence of kin, female social relationships among chimpanzees were originally considered to be weak and of little significance (Goodall, 1986; Wrangham, 1979). However, the role of social bonding among nonkin as an important mediator of social structure in mammalian societies is increasingly being revealed through empirical studies in a variety of species (bottlenose dolphins, *Tursiops aduncus*: Connor, Heithaus, & Barre, 2001; wild dogs, *Lycaon pictus*: de Villiers, Richardson, & van Jaarsveld, 2003; black-and-white colobus monkeys, *Colobus vellerosus*: Wikberg, Sicotte, Campos, & Ting, 2012), and evidence is accumulating that these bonds can have direct fitness benefits in both sexes (male lions, *Panthera leo*: Packer & Pusey, 1982; female feral horses, *Equus caballus*: Cameron, Setsaas, & Linklater, 2009; male Assamese macaques, *Macaca assamensis*: Schuelke, Bhagavatula, Vigilant, & Ostner, 2010; female chacma baboons, *Papio hamadryas ursinus*: Silk et al., 2010). In line with findings from other taxa, there is evidence from multiple study populations of chimpanzees suggesting that females can be more social than traditionally assumed (Lehmann & Boesch, 2008; Wakefield, 2008). For example, Gilby and Wrangham (2008) reported that some female dyads at Kanyawara have as high or higher association rates than the most strongly bonded males, and the highest party association rates among adult chimpanzees at Ngogo (Kibale National Park, Uganda) were recorded for female dyads (Langergraber, Mitani, & Vigilant, 2009). Some suggest that females may indeed form differentiated social relationships that reflect social preferences, like the social cliques identified by Wakefield (2013), and can be stable over time (Langergraber et al., 2009). However, questions remain about whether these relationships are similar to the social bonds among male chimpanzees and philopatric females of other primate societies, and about how females benefit from them.

Here, our main aims were to identify the correlates of female chimpanzee association patterns at Gombe National Park, Tanzania, with particular emphasis on factors that mediate variation in these associations, and to test for the existence of social preferences that could support the existence of social bonds among unrelated females. For this purpose, we analysed the most comprehensive set of behavioural data from any population of wild chimpanzees to date, spanning a period of 38 years.

Detecting and characterizing differentiated social relationships is challenging among female chimpanzees at Gombe, because affiliative interactions are rarely observed (Goodall, 1986). Instead, estimates of social preferences rely heavily on dyadic association indices derived from party composition data (Cairns & Schwager, 1987), that is, information on who was seen with whom. While the fission–fusion nature of chimpanzee social structure offers unique opportunities for individuals to express partner choices within their communities, it poses unique challenges for researchers attempting to distinguish actual social preferences from random associations due to shared space use, a problem shared with studies of other social mammals (tent-making bats, *Artibeus watsoni*: Chaverri, Gamba-Rios, & Kunz, 2007; bottlenose dolphins: Frère et al., 2010; grey kangaroos, *Macropus giganteus*: Best, Dwyer, Seddon, & Goldizen, 2014).

Previous studies on female chimpanzee dyadic association have varied in their approaches to assess the influence of shared space use on association patterns. Some classified similarities in space use at the scale of “neighbourhoods”, and assumed little further influence of variation in core area overlap on association rates within these neighbourhoods (Gombe: Murray et al., 2007; Williams et al., 2002b; Kanyawara: Emery Thompson et al., 2007). In contrast, at Ngogo, Langergraber et al. (2009) used a more spatially explicit technique by testing for a relationship between (1) correlation coefficients representing similarity in grid cell usage frequencies between any two individuals and (2) the party association index for the given dyad. A matrix correlation of the two measures provided evidence that, across all female dyads, shared space was positively related to association rates. Similarly, Wakefield (2013) established that dyadic associations were positively correlated with space use overlap, assessed as the percentage overlap of any two minimum convex polygons drawn around 100% of sightings for a given female.

As association depends on being in the same location at the same time, a positive relationship between degree of shared space use and dyadic association rate is likely, though not guaranteed (e.g. De Villiers & Kok, 1997). Therefore, revealing active partner preferences generally relies on assessing rates of association that deviate from those expected based on random interactions among all individuals sharing the same area. Previous studies on female chimpanzee association patterns established random expectations for dyadic association rates based on permuting the rows and columns of an association matrix (Langergraber et al., 2009; Lehmann & Boesch, 2009; Wakefield, 2013). However, such matrix permutation tests do not account for spatial constraints on association, and are therefore most suitable in social groups where all individuals do indeed share the same space (e.g. Lehmann & Boesch, 2009). If individuals occupy distinct and only partially overlapping home ranges, as is the case for female chimpanzees at Gombe and other East African populations, spatially explicit methods for deriving expected association rates (e.g. Best et al., 2014) may provide a more powerful technique to assess social preferences.