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Social dynamics among females and their influence on social structure in an East African chimpanzee community

Monica L. Wakefield [a,b,*]

[a] Department of Anthropology, Yale University, New Haven, CT, U.S.A.
[b] Department of Anthropology, University of California San Diego, La Jolla, CA, U.S.A.

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Social structure in group-living animals is defined by the nature and patterning of social interactions among members of the society. Social structure is shaped in large part by kinship and competition among group members, but can also be influenced by affiliative interactions among both kin and nonkin and can vary based on sex differences in dispersal patterns and social dynamics. Chimpanzees, *Pan troglodytes*, live in fission–fusion societies in which males form strong dyadic bonds and have social networks that can influence the social structure of the community. Females are generally less gregarious than males and bonding among females is considered rare or absent in East African populations. Although females in some populations are known to form 'neighbourhoods', these are assumed to reflect passive spatial arrangements. In this study I used data on female chimpanzee association and social interactions to examine how social dynamics among the dispersing sex influence social structure at Ngogo, Kibale National Park. Females at Ngogo were relatively gregarious and exhibited association preferences that extended beyond the dyadic level. Females formed distinct association clusters termed 'cliques' within which affiliative interactions occurred more than expected by chance. In addition, association patterns were found to be active social units and not a by-product of space use overlap. These findings demonstrate that intrasexual bonding is not limited to males in this population and that female social relationships, not just those of males, can influence chimpanzee grouping patterns and the corresponding social structure of the community. This study contributes to our growing understanding chimpanzee behavioural diversity.

A fundamental challenge in behavioural ecology is understanding how individual behaviour influences animal societies (Croft et al. 2008; Whitehead 2008). This includes the typical nature of social interactions and social relationships, which make up the social structure of the society (Hinde 1976; Lee 1994). Social structure is often shaped in large part by kinship and dominance relationships among group members (reviewed in Koenig 2002). More recently though, researchers have emphasized the contribution of social attraction and affiliative interactions (in addition to or in conjunction with competition), even among unrelated pairs, in shaping the dynamics of group social structure (e.g. bottlenose dolphins, *Tursiops truncatus*: Lusseau et al. 2006; meerkats, *Suricata suricatta*: Madden et al. 2009; spider monkeys, *Ateles geoffroyi*: Ramos-Fernandez et al. 2009). In societies with sex-biased dispersal patterns, the dispersing sex will have fewer opportunities to interact with kin. Yet, affiliating with nonkin can still have important direct fitness benefits to individuals, such as improved health (Seeman 1996; Thorsteinsson & James 1999) and stress reduction (Sapolsky 1998; Carter et al. 2009), particularly among females (Taylor et al. 2000; Cheney & Seyfarth 2009). Thus, while frequently less understood, examining the dynamics of relationships in the dispersing sex holds great interest.

Populations with sex differences in patterning of gregariousness, social interactions and space use can lead to functionally distinct sex-specific influences on social structure. This is seen at its extreme in societies with patterns of sexual segregation, for example many social ungulates (Main et al. 1996), but sexual segregation can also occur to varying degrees in societies with fission–fusion social organization (Ruckstuhl & Neuhaus 2000). Sex differences in social dynamics that shape social structure have been documented in a diverse array of fission–fusion societies, such as African elephants, *Loxodonta africana* (Moss & Poole 1983), sperm whales, *Physeter macrocephalus* (Whitehead & Weilgart 2000), Galápagos sea lions, *Zalophus wollebaeki* (Wolf et al. 2007), and spider monkeys, *Ateles geoffroyi* (Fedigan 1984). Thus, it is important to understand the patterning of social interactions of both sex classes when analysing social structure (Whitehead 2008).

* Correspondence and present address: M. L. Wakefield, Northern Kentucky University, Department of Sociology, Anthropology, and Philosophy, 1 Nunn Drive, 228 Landrum Academic Center, Highland Heights, KY 41099, U.S.A.
E-mail address: mlwakefield@gmail.com.

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Here I focus on how intrasexual social relationships and affiliative interactions among females influence the social structure of the Ngogo chimpanzee community in Kibale National Park, Uganda. Chimpanzees, *Pan troglodytes*, live fission–fusion groups in which individuals form subgroups called 'parties' (Sugiyama 1968) that are highly fluid and flexible (Reynolds & Reynolds 1965; Goodall 1968; Nishida 1968). Like other species exhibiting fission–fusion social systems, chimpanzees provide a natural framework for analysing variation in social relationships (Aureli et al. 2008). Females are the dispersing sex in chimpanzees (Pusey 1980); thus, there is low variation in the degree of relatedness between females in the same community, and the majority of female–female dyads will not be closely related (Vigilant et al. 2001). In addition, chimpanzees show considerable sex differences in gregariousness and space use patters (Wrangham 1979). Chimpanzee social structure is traditionally characterized by highly gregarious males that form strong intrasexual bonds and by females that spend the majority of their time alone, but this can vary across populations and with temporal fluctuations in food availability (reviewed in Watts 2012). Male dyadic bonds are reflected in affiliative behaviours such as preferential and nonrandom association, proximity and grooming (reviewed in Mitani 2009). These relationships in turn influence male grouping patterns (Halperin 1979; Newton-Fisher 1999, 2002; Mitani & Amsler 2003; Gilby & Wrangham 2008) and can result in social substructuring or social clique formation (Newton-Fisher 1999; Mitani & Amsler 2003). While a few recent studies have reported that females at some sites are relatively gregarious and spend the majority of their time in social parties and 20% or less of their time alone, including both East African, *P. t. schweinfurthii* (Bugongo: Fawcett 2000; Emery Thompson & Wrangham 2006; Ngogo: Wakefield 2008) and West African, *P. t. verus* (Taï: Lehmann & Boesch 2008) subspecies, the traditional view of chimpanzee social structure still holds strong in the literature (e.g. see Mitani 2009). Competition among and dominance relationships between females have received much attention from researchers (e.g. Pusey 1983; Williams et al. 2002b; Wittig & Boesch 2003; Murray et al. 2006; Newton-Fisher 2006; Emery Thompson et al. 2007), but quantitative data on affiliative social interactions between females remain rare in the literature (but see Lehmann & Boesch 2009); social relationship dynamics among female East African chimpanzees in particular and how they contribute to chimpanzee social structure remain poorly understood.

In societies with flexible grouping patterns, dyadic associations are thought to reflect social relationships and preferences among individuals (e.g. African buffalo, *Syncerus caffer*: Cross et al. 2005; Asian elephants, *Elephas maximus*: de Silva et al. 2011; bottlenose dolphins, *Tursiops* spp.: Gero et al. 2005; spotted hyaenas, *Crocuta crocuta*: Holekamp et al. 1997). However, association patterns could form randomly or passively, even among dyads with higher-than-expected association frequencies (e.g. Ramos-Fernandez et al. 2009), and thus do not always reflect active social preferences (Newton-Fisher 1999). For example, party membership could reflect aggregations at mutually attractive resources, rather than attraction to conspecifics (dusky dolphins, *Lagenorhynchus obscurus*: Pearson 2009; orang-utans, *Pongo pygmaeus*: Sugardjito et al. 1987; chimpanzees: Wrangham 1977), or association patterns could be a by-product of limited ranging flexibility and/or site fidelity (e.g. false killer whales, *Pseudorca crassidens*: Baird et al. 2008; Galapagos sea lions, *Zalophus wollebaeki*: Wolf & Trillmich 2007). Thus it is important when analysing animal social structure to distinguish between active versus passive or random association (e.g. Mitani et al. 1991; Whitehead 1997; Bejder et al. 1998; Newton-Fisher 1999; Whitehead & Dufault 1999). Both of these factors have the potential to influence female chimpanzee grouping patterns. Females in some East African communities form spatial clusters known as 'neighbourhoods' in which a subset of females have overlapping core ranging areas in the same general part of their community's territory (Kanyawara: Emery Thompson et al. 2007; Mahale: Hasegawa 1990; Gombe: Williams et al. 2002b). Females show strong site fidelity to core areas (Murray et al. 2007) and, if range overlap compounded by shared resources within their ranges increases the likelihood that two individuals are found together, then association frequencies could be a by-product of range overlap rather than an expression of social affinity (Gilby & Wrangham 2008).

The aims of this paper are two-fold. First, I used data on party formation to test the null hypotheses that female association patterns reflect passive or random aggregations resulting from (1) mutual attraction to resources and/or (2) a by-product of space use overlap compared to the alternative hypothesis that female association patterns reflect active social preferences (sensu Newton-Fisher 1999). Second, I analyse association patterns to investigate female social structure and to explore whether females form social bonds that exist at a higher level than the dyadic pair, as found in male chimpanzees in the unusually large Ngogo community (Mitani & Amsler 2003). I expand on previous reports of female substructures at Ngogo (Wakefield 2008; Langergraber et al. 2009) to examine the social component of these units. I use data on affiliative (proximity and grooming) and agonistic social interactions to investigate the social dynamics of female social structure to test the hypotheses that (1) female substructures represent active social units based on mutual affinity and (2) rates of agonism are lower among frequent associates due to stable dominance relationships (Emery Thompson et al. 2007). Proximity and grooming patterns are widely considered effective measures of the value of social relationships in primates (Cords 1997) and are accordingly commonly used to meaningfully evaluate social bonds (e.g. female chimpanzees, *P. t. verus*: Lehmann & Boesch 2009; male chimpanzees, *P. t. schweinfurthii*: Newton-Fisher 2002; white-faced capuchins, *Cebus capucinus*: Perry 1996; female baboons, *Papio cynocephalus*: Silk et al. 2006).

METHODS

Study Site and Animals

I observed chimpanzees at the Ngogo research site, Kibale National Park, Uganda for 19 months between April 2003 and May 2004 (Period 1) and between October 2004 and June 2005 (Period 2). Ngogo is in the centre of Kibale in an area transitional between lowland and montane rain forest that consists primarily of moist mature evergreen and regenerating forest (Ghiglieri 1984; Butynski 1990; Struhsaker 1997).

The Ngogo community is the largest known chimpanzee community and, at the start of my study, the community included 44 adult females, 6 adolescent females, 26 adult males, 13 adolescent males, 22 juveniles and 29 infants. I selected 24 well-habituated females, including individuals of varying ages and some with and others without infants, as targets for focal data collection (total focal observation time = 1418 h; see Appendix). Twenty-one targets were parous adults at the start of data collection, two were nulliparous, but became pregnant during the first period of data collection, and one adult female was infertile and never cycled. Of the 276 dyads included in my sample, two were mother–adult daughter dyads (EK and CA; ME and HL) and the remaining 274 dyads were not close kin (Langergraber et al. 2009).

Data Collection

I used several methods to locate target females and to minimize biases towards larger parties, including listening for calls, checking fruiting trees and systematically searching the study area (Chapman et al. 1993). I collected data using a combination focal