Stable and fluctuating social preferences and implications for cooperation among female bonobos at LuiKotale, DRC

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ABSTRACT

Objectives

Female bonobos (*Pan paniscus*) are typically characterized as having affiliative and cooperative relationships, but it is not known if females are selective in their choice of social partners, or whether their relationships are relatively undifferentiated. Our goals were to measure social preferences among wild female bonobos, to identify factors that influence variation in social preferences among females, and to test whether social preferences predict patterns of cooperation in food sharing or providing coalitionary support.

Materials and Methods

We collected behavioral data over three years among resident female members of the Bompusa community at LuiKotale, DRC. We used genetic analyses to determine the extent of relatedness among subjects. We constructed social preference indices for party association, proximity, grooming, GG-rubbing and aggression, used permutation tests to identify preferred social partners and tested whether variation in preferences was consistent across different behaviors and stable over years. We performed a factor analysis to identify meaningful inter-relationships between the various social preference indices and used GLMMs to test whether variation in social preferences was explained by extent of relatedness, rank distance, co-occurrence of dependent young or co-residency

time between females. We then tested whether variation in social preference indices predicted patterns of food sharing or coalitionary support among females.

Results

Nine of the 78 focal dyads (11.5%) shared mtDNA haplotypes, including two mother-adult daughter dyads. All N=13 females had at least one preferred non-kin partner for staying in close proximity, grooming or GG-rubbing, but only grooming preferences were stable from year to year. Association indices were higher among lactating females, and aggression decreased among females who had co-resided in the community for longer. Variation in proximity, grooming and GG-rubbing preferences were not explained by any of the female attributes that were tested. The factor analysis identified one dimension of female social relationships, based on the combined proximity and GG-rubbing preferences, that we interpreted as a measure of behavioral coordination. Dyads with higher levels of behavioral coordination were more likely to share food with each other.

Discussion

Female bonobos exhibit differentiated and stable grooming relationships outside of kinship and philopatry. Females also maintain high levels of behavioral coordination with a large and flexible network of social partners who are more likely to share food with each other. Maintaining different types of stable and flexible social relationships may help female bonobos to achieve cooperation with a wider range of social partners.

Female dispersal is more widespread in primates than typical of mammals (Strier, 1994) occurring habitually in several species of colobines and atelines and in all three African apes (reviewed in Lee and Strier, 2015). Early socio-ecological models assumed that variation in female sociality within primate groups was primarily determined by the distribution of resources and the intensity of feeding competition (reviewed in Clutton Brock and Lucas, 2011). Dispersal was considered adaptive for females only when levels of within and between-group feeding competition were sufficiently low that intra-sexual alliances were no longer important for defending food, making nepotistic ties less important and leading to relatively undifferentiated relationships among females (Wrangham, 1980; Sterck, Watts & van Schaik, 1997; Isbell & Young, 2002). These early models contrast with a growing body of empirical research indicating a high degree of intra- and inter-specific variation in social behaviour among dispersing females, including evidence for cooperative and competitive social dynamics (Furuichi, Yamagiwa and Aureli, 2015). For example, dispersing female spider monkeys (*Ateles geoffroyi*) are typically characterized by weak intra-sexual relationships (Aurelli and Schaffner, 2008), but exhibit marked increases in association and affiliation while lactating (Shimooka, 2015; Slater, Schaffner and

Aureli, 2007) and females cooperate with each other to defend food resources, typically from more recent immigrant females (Slater, Schaffner, & Aureli, 2009). Across several chimpanzee study sites, dispersing females exhibit stable, preferential patterns of association as dyads (Lehmann & Boesch, 2009; Langergraber et al., 2009; Foerster et al., 2015) or larger cliques (Wakefield, 2013), and preferential associates also engage in higher than expected levels of affiliative grooming at some sites (Langergraber et al., 2009; Wakefield, 2013; Foerster et al., 2015), although cooperation in other contexts is rare (Langergraber et al., 2009). Research on the diversity of social relationships among dispersing female primates is helping to expand socio-ecological models by including factors beyond ecology that can influence dispersal decisions (Koenig, 2002; Clutton-Brock and Janson 2012) and by identifying factors outside of kinship that can promote cooperation, for members of the philopatric and dispersing sex (Candiotti et al., 2015; Lee and Strier, 2015).

A better understanding of the causes and consequences of variation in social relationships among female bonobos can provide further insights into how cooperation can be achieved outside of kinship and philopatry. Bonobos live in large, mixed-sex communities characterized by female-biased dispersal (Lomako: Eriksson et al., 2006; Gerloff, Hartung, Fruth, Hohmann and Tautz, 1999; Wamba: Hashimoto, Takenaka and Furuichi, 1996, LuiKotale: this study), with only rare cases in which females remain in their natal communities after maturity (Hashimoto, Takenaka and Furuichi, 1996). Bonobos also exhibit flexible fission-fusion grouping patterns, in which members of a community break up into sub-groups, or parties, of fluctuating size and composition. Despite being the dispersing sex, female bonobos prefer to associate together (White 1986; White & Burgman, 1993), resulting in a greater proportion of total female community members present in daily parties (27-53%, see Table 1) in comparison with female chimpanzees (e.g. 6% at Kalinzu Forest, Uganda, reviewed in Furuichi, 2009). Among the E1 community at Wamba, females are also disproportionately represented in parties relative to male bonobos (reviewed in Furuichi, 2009). Female bonobos also cooperate in a range of contexts, including co-defending and sharing access to food resources (Hohmann & Fruth, 1996; White & Wood, 2007) and supporting each other in coalitionary aggression that is often directed against males (Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016). Several theories suggest that high levels of association provide more opportunities for females to engage in cooperative alliances that provide competitive advantages over males (Clay et al., 2016; Furuichi 2011; Jaeggi et al., 2016). Females also experience intra-sexual conflicts over access to mating opportunities (Hohmann & Fruth, 2003), struggles to increase social status (Furuichi, 1997), or when defending offspring from conspecific aggression (L. R. Moscovice, unpublished data). Although rare, when female intra-sexual aggression does occur it is sometimes expressed bi-directionally (Furuichi, 1997) and often triggers coalitionary support, suggesting that female aggression may represent serious conflicts. The combined evidence suggests that females may benefit from engaging in differentiated relationships to mitigate intra-sexual competition and to facilitate intra-sexual cooperation.

Indeed, female bonobos in captive and field settings are often characterized as having highly affiliative social bonds (e.g. Parish, 1996; Tokuyama & Furuichi 2016), but few studies that have attempted to quantify variation among females in the strength and stability of their social relationships and to determine how variation in female social relationships influences patterns of cooperation. In addition, little is known about variation in female sociality across communities and study sites, which may have important implications for patterns of cooperation (see Table 1). Across sites, females engage in diverse social interactions including affiliative grooming, which can occur among a large proportion of female dyads (Sakamaki, 2013) and genito-genital rubbing (or GG-rubbing), a common socio-sexual behavior among females, in which partners embrace and rub their genitals together. GG-rubbing has been implicated in reducing social tension and coordinating behavior (Hohmann et al. 2009; Idani 1991; Douglas and Moscovice 2015). At the Lomako study site, DRC, differentiated relationships were identified using measures of party association and feeding proximity (White & Burgman, 1993) or party association and grooming (Hohmann, Gerloff, Tautz and Fruth, 1999), but in the only study to measure stability, social preferences were found to fluctuate over time and were considered to be opportunistic (Hohmann, Gerloff, Tautz and Fruth, 1999). At Wamba, a three-month study failed to find evidence for differentiated social relationships among long-term resident females, although recent immigrants and long-term residents had differentiated relationships based on above expected measures of proximity and GG-rubbing (Idani, 1991). [Insert Table 1].

The goals of this study are to quantify social preferences for association and affiliation among all resident female members of the habituated Bompusa bonobo community at LuiKotale, DRC, to identify stable attributes of females that influence variation in social preferences and to determine whether variation in social preferences predicts patterns of dyadic cooperation in two contexts: Food sharing and providing coalitionary support. We hypothesize that females will exhibit stable preferences to associate and affiliate with a subset of partners and that social preferences will be consistent across several affiliative behaviors and stable across years. Such evidence would add to a growing literature indicating that selective, affiliative relationships occur outside of kinship and philopatry in some primate species (female chimpanzees: Langergraber et al., 2009; male Assamese macaques: Kalbitz, Ostner, & Schülke, 2016). We further hypothesize that social preferences will be influenced by one or more of the following dyadic attributes: 1) Extent of genetic relatedness, 2) Differences in dominance rank, 3) Presence of dependent young, or 4) Extent of co-residency time in the community. Although rare, genetic analyses confirm some cases in which female bonobos remain in their natal communities and reside with close maternal relatives (Gerloff et al., 1999, Hashimoto, Takenaka and Furuichi, 1996). It is thus possible that female bonobos prefer to associate and affiliate with relatives when they have opportunities to do so. Interestingly, a previous study at Wamba found no differences in measures of affiliation among non-kin and a subset of related females (Hashimoto, Takenaka and Furuichi, 1996). Evidence from additional bonobo communities is needed to further investigate whether this may reflect a species difference in reliance on nepotistic ties between female bonobos and female chimpanzees, who tend to form the strongest social bonds with relatives when they are present (e.g. Foerster et al., 2015; Langergraber, Mitani & Vigilant 2009).

When kin are not available, members of the philopatric sex form stronger social relationships with individuals of similar dominance rank (e.g. Silk, Altmann and Alberts, 2006), who share more similar social interests and may make the most effective allies outside of kin relationships (reviewed in Silk, 2009). There is evidence that female bonobos socialize more when they are lactating (Waller, 2011), which may be a strategy to invest in relationships with other females who have similarly-aged offspring, leading to increased opportunities for socialization of their young (Williams, Liu and Pusey, 2002). In the dispersing sex, it is also possible that social preferences develop gradually over time and will be strongest among females who have resided together in the same community for longer. Finally, if female bonobos do exhibit differentiated relationships, we hypothesize that more preferred partners will be more likely to cooperate in other contexts, including providing coalitionary support or food sharing.

Alternatively maintaining highly individuated relationships with a relatively small number of partners may not be an adaptive strategy for female bonobos, given that the availability of female social partners is likely to change on a daily basis, due to fission-fusion social dynamics and on a more long-term basis due to immigration and emigration events. In this social environment, females may benefit by flexibly shifting their social investment among different partners in response to short-term contingencies, leading to more balanced, undifferentiated relationships over the long-term. Cooperation may also emerge in the absence of differentiated social relationships, if it represents mutualisms providing shared benefits to all participants (Clutton Brock, 2009).

MATERIALS AND METHODS

Study site and data collection

Data were collected between June 2011 and June 2014 during focal follows of all N = 13 mature resident female members of the Bompusa community at the LuiKotale field site, situated near the southern sector of Salonga National Park, Democratic Republic of Congo. The core study site consists of a network of transects covering approximately 50 sq kilometers of lowland rainforest habitat

(Hohmann and Fruth, 2003), although the community can also range outside of this core area. Habituation of the Bompusa community began in 2003 (Hohmann and Fruth 2003) and behavioral data has been collected continuously since 2007 from all resident adult and sub-adult community members. During the three-year study period, the community consisted of between 36–40 individuals, including 13 mature, resident females, 7 mature males, 11–22 immature individuals and eight nulliparous, immigrant females who temporarily associated with the community for varying periods of time (median= 2 months, range= 0.57–8.47 months). Mature females were defined as parous females who had resided in the community continuously for at least one year at the beginning of the study. These included eight females who were present in the community since the habituation began in 2003 (long-term residents), three females who were first confirmed in the community in 2007 (intermediate residents) and two females who immigrated into the community during 2010 (short-term residents). Of the long-term residents, the two youngest were confirmed via genetic analyses to be have been born in the community. Both gave birth to their first offspring during the study period. Following Douglas et al. (2016), mature males were estimated to be ≥ 10 years of age. Immature individuals were < 10 years of age.

Over 2700 focal observation hours were collected by LRM (2011 & 2013–2014), PHD and assistants (2011–2013), and LMI and MS (2013–2014). Focal observation time was similar between year one (beginning in June 2011–May 2012) and year two (June 2012–May 2013, 1009 vs. 1158 focal hours), but was reduced in year three (June 2013–May 2014, 604 focal hours) due to extensive ranging outside of the core study area where the researchers were not permitted to enter. Focal females were observed for mean ± SD = 218 (± 171) hours (see Table 2). Variation in observation time was due to differences in priority subjects for focal sampling across years, and also because one natal female (Po) was absent from Aug–Dec 2011. During focal observations, we used focal scan sampling to record the focal's main activity (traveling, feeding, resting, grooming) at 5-mn intervals and the identity of all individuals within close proximity to the focal subject at 15-minute intervals. Close proximity was defined as being within 2 m, since this was less than the average inter-individual distance between females (3.7 ± 2.4 m, based on N = 2897 scans where the distance of females' neighbors up to 10 m were recorded) and thus more likely to reflect active preferences. We also recorded continuous focal data on independent GG-rubbing events (separated by an interval of ≥ one minute between events involving the same dyad), between focal subjects and other females. Presence in parties was updated continuously during focal observations, and summarized at the end of a 30-minute sample period, during which all individuals seen within the preceding 29 minutes were considered to be in the same cumulative party scan. Although this approach may over-estimate association time among individuals who may fission for brief periods, it was necessary due to limitations in the ability to observe all members of a party that were often spread out over a large area while still coordinating their travel. We also recorded changes in party composition during fission and fusion events.

We recorded all-occurrence data on less frequent social events including all independent cases (separated by an interval of ≥ one minute between events involving the same dyad) of aggression, coalitionary support and food sharing. Aggression included directed displays, chases or contact aggression, including holding, hitting or biting, where the intended target was clearly identifiable. Female dominance rankings were based on cumulative data on all occurrences of aggressive interactions with decided outcomes over a four-year period, including the three years of this study. To determine female rankings, we used the ADAGIO algorithm, developed by Douglas and colleagues (*in press*). ADAGIO is a novel method for assessing dominance that computes directed acyclic graphs from interaction matrices to represent dominance relationships. ADAGIO differs from other commonly used dominance ranking methods in that it does not assume totality, allows for tied relationships, and accounts for structural zeros in the interaction matrix. As a result, this method is appropriate for assessing dominance dynamics in social groups that do not have a strongly linear dominance structure. This appears to be the case for female bonobos, who have infrequent and sometimes intransitive aggressive interactions (e.g. Furuichi, 1997; Surbeck and Hohmann, 2013). ADAGIO results in rankings that reflect these characteristics and can be interpreted as dominance levels in which multiple individuals may occupy the same rank level.

Female coalitionary support occurred when one female supported another in an aggressive attack on a third party. Support included vocal aggression, chasing and/or contact aggression that occurred in a coordinated fashion as the attacker directed one or more of those behaviors at a third party. Polyadic coalitions (involving more than two coalition partners) were excluded since the intended target of support was not always clear. Food sharing involved passive or active transfer of a potentially monopolizable food from a food possessor to a bystander. Most cases of food transfer were passive, whereby bystanders took pieces of food directly from a food source (e.g. honey from stingless bees, fruit of *Treculia africana* or *Anonidium mannii*, or meat from duikers (*Cephalophus* sp.) or water chevrotains, *Hyemoschus aquaticus*) that another individual possessed. In some cases, two females shared possession and fed simultaneously from the same monopolizable food source.

Measuring social preferences

We measured preferences for association in parties based on each female's choice of partners during independent fission events (e.g. Cross, Lloyd-Smith, & Getz, 2005). A fission event occurred when two or more females separated from the original party and remained undetected (i.e. outside of visual and auditory range) for at least an hour. A total of N = 207 fission events met these criteria. These fissions occurred on 28.1% (N = 179) of total observation days where full day party scans were collected (N = 638). On days with fissions, they typically occurred 1.17 (± 0.44) times. We calculated the association preference index as: $AB_{\text{Post-fission}} / AB_{\text{Pre-fission}}$, where $AB_{\text{Post-fission}}$= number of times that A and B were observed in a party after a fission event, and $AB_{\text{Pre-fission}}$ = number of times that A and B were observed in a party before a fission event. By measuring preferred partners only at fission events, this index avoids temporal auto-correlation issues that arise through repeated measures of co-occurrence in parties and may also be more likely to reflect true social affinities rather than more passive associations that occur as a byproduct of shared interests, for example to forage in the same areas (Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007).

We used additional sociality indices originally developed for chimpanzees (Gilby & Wrangham, 2008) that account for individual differences in focal observation time and party attendance. We modified these indices to also account for differences in individual gregariousness, by measuring the frequency with which two individuals engage in a given target behavior, relative to the frequency that either individual engages in the same behavior with any resident female. The target behaviors included: 1) Proximity, based on the number of focal scans during which two individuals were within two meters while engaged in any activity other than grooming, 2) Grooming, based on the number of focal scans during which females groomed each other, and 3) GG-rubbing, based on the number of independent GG-rubbing events involving the focal female. Each preference index was calculated as: $(A_f(AB_{tb}) + B_f(AB_{tb})) / (A_{f+tb}(B_p) + B_{f+tb}(A_p))$, where

$A_f(AB_{tb})$= number of times that A is the focal (f) and A and B exhibit the target behavior (tb); $B_f(AB_{tb})$= number of times that B is the focal and A and B exhibit the target behavior; $A_{f+tb}(B_p)$= number of times that A is the focal and exhibits the target behavior with any female while B is in the party (p); and $B_{f+tb}(A_p)$= number of times that B is the focal and exhibits the target behavior with any female while A is in the party. We also calculated an aggression index based on all occurrences of dyadic contact aggression, chases or directed displays when the target of the aggression was clearly discerned and the targeted individual responded either with submissive behaviors (e.g. displacement, retreat) or with counter-aggression. The aggression index was calculated as: AB_{agg} / ($A_{agg}(B_p)$ + $B_{agg}(A_p)$), where AB_{agg} = all occurrences of aggression (agg) between A and B, $A_{agg}(B_p)$ = all occurrences of aggression by A to another female when B was in the party (p) and $B_{agg}(A_p)$ = all occurrences of aggression by B to another female when A was in the party.

Each preference index ranges from 0–1, with 0 indicating that females A and B never engaged in the specific social behavior during focal observations, despite having opportunities to do so, and 1 indicating that when females A and B were present in the same party and engaged in the target behavior, they always chose each other as partners. By accounting for individual differences in gregariousness, these indices better reflect true partner preferences and not merely similar tendencies to associate or affiliate more generally (Godde, Humbert, Côté, Réale, & Whitehead, 2013). However, each preference index was highly correlated with the corresponding sociality index that did not correct for individual gregariousness (Mantel, r = 0.85–0.87, P = 0.001), suggesting that correcting for individual gregariousness did not alter the results.

Genetic analyses

As part of ongoing research at LuiKotale, we collected 3-4 fecal samples from all community members and some members of neighboring communities for relationship determination. In previous work we detailed the genotyping of 39 bonobos and the process of paternity assignment for five offspring (Schubert et al., 2013). Samples were stored in RNAlater as previously described (Nsubuga et al., 2004). DNA was extracted using the QIAamp® DNA Stool Mini Kit (QIAGEN). We first centrifuged 2 mL of faeces–RNALater mixture for 15 min at 3000 *g* and discarded the supernatant, then employed a second centrifugation for 15 min at 500 *g* and discarded the supernatant. We then resuspended the pellet in 1.6 mL ASL buffer, vortexed it, and incubated it for 5 min at room temperature. The subsequent steps followed the manufacturer's protocol, and the final volume of ~200 µL per extract was aliquoted and stored at −20 °C. Two negative extraction controls were processed along with each set of 10–15 faecal extracts. We previously genotyped chimpanzee and bonobo extracts at 19 highly-variable microsatellite loci with sufficient replication to ensure accurate results (Schubert el al., 2013; Arandjelovic et al., 2009). For this study we genotyped 31 bonobos at a subset of 13 of the previously-characterized microsatellite loci using an updated multiplex protocol described recently (McCarthy et al., 2015). Four of these 31 individuals had been previously genotyped, and were retyped to ensure that allele identification was consistent between studies. Parentage (maternity) analysis was conducted as previously described by using both mismatch analysis and likelihood analysis approaches in CERVUS 3.0 (Kalinowski et al. 2007).

We then used one DNA extract per female to amplify a 470 bp portion of the hypervariable region of the mtDNA control region using the primers L15996 (CTCCACCATTAGCACCCAAAG) and H16498 (CCTGAAGTAGGAACCAGATG) (Vigilant et al., 1989). For amplification a 3 min initial denaturation step at 97° C was followed by 40 rounds of 30 s at 95° C, 30 s at 60° C and 30 s at 72° C. with a final 30 min at 72° C. Each extract was amplified in duplicate. We measured DNA concentration of amplicons using the NanoDrop system with the Software ND-1000 (version 3.8.1). We sent 20 µl of each amplicon, which represented a total minimum DNA concentration of at least 200 ng, to GATC Biotech AG (European Custom Sequencing Centre, Gottfried-Hagen-Straße 20, 51105 Köln, Germany) for SUPREMErun 96 Sanger sequencing. This produced for each amplicon a forward and reverse sequence. The two forward and reverse sequences for each individual were aligned using Bioedit (version 7.2.5) and trimmed to the same length for further process. Highly repetitive parts of these four sequences were deleted, resulting in a 339 or 340 bp long fragment used for generating a consensus sequence for each individual. The AB1 chromatogram was used to detect base miscalling and to identify the true nucleotides for any instances when a position in the forward and reverse or two replicate sequences generated for each individual differed. Identification and sorting of the different haplotypes was done using the online program FaBoX (Villesen, 2007).

Statistical Analyses

Analyses were conducted in R (version 3.3.0, R Core Team 2016). To characterize the extent of selectivity in partner choice for different social behaviors, we visually inspected the distributions of dyadic scores for each preference index and used two-sample Kolmogorov-Smirnov (KS) tests to determine whether the distribution of scores for each index differed significantly from the others. Due to non-independence of the dyadic measures we derived significance levels for the KS tests using permutation tests created by Roger Mundry, in which columns of data were permuted between matrices. We ran 1000 permutations and determined significance levels based on the proportion of permutations revealing a KS test statistic at least as large as that of the original data. To identify preferred social partners, we calculated expected dyadic scores for each preference index using randomization techniques that controlled for individual differences in observation time and gregariousness, by reshuffling the identity of interaction partners while keeping the number of scans per individual and the composition of the parties from which each individual’s possible partners were selected consistent with the observed data. Mean expected dyadic scores were calculated based on N = 1000 permutations and compared to the observed scores to obtain significance levels. P-values < 0.05 indicated dyads with preference indices significantly above or below expected values, and these dyads were considered to to have “preferred” and “weak” social relationships respectively. Since the permutation tests follow a normal distribution, a certain number of significant results will occur by chance. We used one-tailed binomial tests with unequal proportions to test whether the number of observed preferred and weak dyadic relationships for each preference index differed from the number expected by chance.

To determine whether females’ preferences were stable over time, we calculated yearly preference indices for each social behavior and used Mantel tests to compare the correlations within each index across the three years of the study. For the stability tests, we reduced the data set as necessary to include only the individuals who performed the target behavior in each other’s presence during both of the years being compared (see results Table 4).

To determine whether females had consistent social preferences across different social measures, we compared the correlations among association, proximity, grooming, GG-rubbing and aggression preference indices using Mantel tests in the package “vegan” (Oksanen et al., 2015) with Spearman correlation coefficients. We also used exploratory factor analysis (FA) to determine whether the various preference indices could be reduced to a smaller number of components representing different dimensions of social relationships. Similar methods have been used to identify different dimensions of social relationships in captive bonobos and chimpanzees (Fraser, Schino, & Aureli, 2008; Stevens, Groot, & Staes, 2015). We chose FA over principal components analysis (PCA) since FA is deemed more appropriate for identifying unobservable dimensions of complex variables such as social relationships and is less likely to inflate factor loadings compared to PCA (Budaev, 2010). We ran a FA using the package “rela” (Chajewski, 2009), with varimax rotation aimed at reducing redundancy among the various preference indices. We included in the FA the proximity, grooming, GG-rubbing and aggression indices, based on evidence that these indices (but not the association index) were useful in differentiating more and less preferred social partners (see results section). The grooming, GG-rubbing and aggression indices were square-root transformed to achieve symmetrical distributions. Two tests of sampling adequacy, the Kaiser-Meyer-Olkin (KMO) measure (0.62) and Bartlett’s test of sphericity (X_6= 33.34, P < 0.001), confirmed that the data were appropriate for FA. Following established criteria, we extracted components with eigenvalues > 1 and considered coefficients of correlation > 0.5 or < -0.5 as interpretable, consistent with recommendations for small sample sizes (Budaev, 2010).

We used LMMs with gaussian error structure to determine whether dyadic variation in social preference indices (response variables) was influenced by the following social factors (test predictors): 1) Scaled rank distance, calculated as: (Dyadic rank distance$_{AB}$ - Dyadic rank distance$_{min}$) / (Dyadic rank distance$_{max}$ - Dyadic rank distance$_{min}$); 2) Duration of observation time during which both females had offspring less than four years of age, based on evidence that most young are weaned by that age (De Lathouwers and Van Elsacker, 2006; Oelze, 2015). 3) Dyadic co-residency time, categorized as short, medium or long; and 4) Putative maternal relatedness, based on results of the genetic analyses. To account for potential influences of adult sons on female social behaviour (e.g. Surbeck, Mundry and Hohmann, 2011), we included whether each female had an adult son (categorical) as a control predictor. We used GLMMs with binomial error structure to determine whether the likelihood that dyads engaged in food sharing or coalitionary support during the study period (response variables) were predicted by the social preference indices. We included dyadic co-observation time (the total time that either member of the dyad was the focal while the other was present in the party) as an offset term in the GLMMs, to insure that results did not merely reflect differences in opportunities to observe dyads cooperating. In both LMMs and GLMMs, predictors were transformed when necessary to achieve approximate normality. The identity of each individual in the dyad was included as a random effect. To reduce the possibility of inflated type I error rates, we also included random slopes of all test predictors that varied within individuals. This method accounts for additional random variance that may influence the response variables (Barr, Levy, Scheepers and Tily, 2013). LMMs and GLMMs were conducted using the package ‘lme4’ (Bates, Maechler, Bolker and Walker, 2015). We confirmed that the models were stable by comparing the estimates derived from a model based on the full data set with those obtained from a model with each subject excluded one by one. We also used the “vif” function in the package “car” (Fox and Weisberg, 2011), to test for variance inflation and found no evidence for collinearity of the predictors. We then used likelihood ratio tests to compare each model to a null model excluding the test predictors and present results of models that differed significantly from the null. Results are presented as mean ± SD unless otherwise stated.

RESULTS

Genetic Analyses

Our microsatellite genotyping of the focal females showed that for two pairs of females, each shared an allele at every locus, consistent with a parent-offspring relationship. One of these pairs was a suspected mother-daughter dyad (Pa-Po), while the other relationship was previously unknown (Ri-Lu). With the exception of parentage analyses, assessment of other possible genetic relationships between adult individuals is challenging and error-prone (eg. Staedele & Vigilant 2016). We therefore characterized mitochondrial DNA (mtDNA) variation for each of the females in the study. Because mtDNA is maternally inherited, we expect that members of a dyad with dissimilar mtDNA sequences could not be maternal relatives, while individuals with identical mtDNA sequences are maternal relatives of unknown degree. We obtained sequences of ~340 bp of the HV1 segment of the mtDNA control region from the 13 focal females and identified seven different haplotypes. Nine of the 78 focal dyads (11.5%) shared mtDNA haplotypes, including as expected the two confirmed mother-daughter dyads. The additional seven dyads with identical mtDNA haplotypes (Gw-Pa, Gw-Po, Gw-Um, Ir-Na, Pa-Um, Po-Um, Su-Zo) represent potential maternal relatives of unknown degree. All other dyads were categorized as unrelated (see Figure 2).

Variation in the strength of partner preferences across different social behaviors

Females were most often in mixed sex parties (91.1 (± 4.0) % of party scans) and less frequently in parties containing only other mature females (8.4 (± 3.8) % of scans, see Table 2). On only rare occasions were females observed apart from other mature females or males, associating only with their sub-adult or immature offspring (< 1% of party scans). During the observation period, focal females groomed with 8 (± 3) different females or 64 (± 26) % of possible female partners, and GG-rubbed with 11 (± 1) partners, or 92 (± 11) % of possible females. There were N = 184 independent occurrences of dyadic intra-sexual aggression, and each female was involved in 28.6 (± 19.1) aggressive interactions (as either the aggressor or victim) with other females. Females were involved in aggression with 9 (± 2) different females, or 78 (± 15) % of possible females. [Insert Table 2 here].

The association and proximity preference indices had similar, symmetrical distributions and variances and did not differ significantly from each other (KS, d = 0.19, P = 0.05, see Table 3). In contrast, the grooming, GG-rubbing and aggression preference indices had right-skewed distributions with greater variances in index values, and all three indices differed significantly from the association and proximity indices (KS, d=0.40–0.59, p< 0.002, see Fig. 1 and Table 3). The more right-skewed distributions were due to a large number of dyads that were rarely observed in grooming, GG-rubbing or aggressive interactions, and a subset of dyads in which individuals preferentially targeted each other for affiliative or agonistic behaviors. [Insert Figure 1] [Insert Table 3]

The percentage of dyads with association preference scores significantly higher or lower than expected values did not differ from the number predicted by chance (binomial tests, $P \geq 0.05$, see Table 3). However, a larger percentage of dyads than predicted by chance had index scores significantly higher or lower than expected for proximity (binomial tests, $P < 0.001$), grooming (binomial tests, $P < 0.001$) and GG-rubbing (binomial tests, $P = 0.01$), indicating that a subset of females selectively targeted each other for these behaviors, while avoiding other potential partners. More dyads had significantly higher (binomial test, $P < 0.001$)

but not lower (binomial test, *P* = 0.13) aggression preference scores than expected by chance, indicating that females also selectively targeted certain individuals for aggressive interactions (see Table 3). Although 22 dyads (28 %) exhibited preferences to stay in close proximity, GG-rub or groom that were significantly above expected values, only seven dyads (9 %), representing N = 11 females, were preferred partners for more than one of these indices (see Fig 2). Similarly, only seven dyads (9 %), representing N = 10 females, exhibited significantly weaker relationships than expected across more than one index. Thus, over the three-year period few females consistently targeted the same partners for all socio-positive behaviors, nor did many dyads consistently avoid engaging in any kinds of socio-positive behaviors with each other. Importantly, every female had at least one preferred social partner for proximity, grooming or GG-rubbing, and several had (typically distinct) preferred partners for all three behaviors (see Table 2 and Fig. 2). Interestingly, none of the confirmed maternal relatives, including two mother-adult daughter dyads, were preferred partners for any of these behaviors (see Fig. 1 and Fig. 2). Preferred partners for socio-positive behaviors did not necessarily avoid aggressive interactions. Of the nine dyads with significantly higher than expected aggression indices, five of these dyads (56 %) were also preferred partners for either grooming (N = 2), GG-rubbing (N = 1) or both (N = 2).

Stability in partner preferences for different social behaviors

The dyadic grooming preference indices remained stable between consecutive years (Mantel tests, $r = 0.49–0.53$, $P \leq 0.05$, see Table 4). However, the preference indices for association, proximity, GG-rubbing and aggression fluctuated from year to year, indicating more flexibility in dyadic preferences for these behaviors over time (Mantel tests, see Table 4) [Insert Table 4].

Consistency between different social preference indices

The strongest correlations among preference indices involved the proximity index with association, grooming and GG-rubbing indices (Mantel tests, $N = 78$ dyads, proximity and association, $r = 0.34$, $P = 0.003$; proximity and GG-rubbing, $r = 0.40$, $P = 0.001$; proximity and grooming, $r = 0.37$, $P = 0.001$). Grooming preferences were also correlated with association ($r = 0.28$, $P = 0.006$) and GG-rubbing ($r = 0.30$, $P = 0.006$) preferences. Aggression was not strongly correlated with any of the other measures ($r = -0.002–0.19$, $P > 0.08$). In the factor analysis in which proximity, grooming, GG-rubbing and aggression preference indices were included, the best solution retained one factor that explained 30 % of the variance in the original data (see Table 4). This factor had strong loadings of proximity ($r = 0.72$) and GG-rubbing ($r = 0.63$) and we interpreted this factor as representing dyads that are able to maintain high levels of behavioral coordination within sub-groups, by staying in close proximity and using GG-rubbing when necessary to mitigate social conflicts. Grooming and aggression had weak loadings on the extracted factor (see Table 5), indicating that neither measure helped to explain this factor. Additional factors had eigen values less than one, and were uninterpretable. In subsequent models investigating the causes and consequences of different social preferences for females, we include the dyadic scores from the FA, indicating variation in combined proximity and GG-rubbing preferences, as a measure of dyadic tolerance and behavioral coordination. However testing proximity and GG-rubbing preferences separately in models did not alter the results. [Insert Table 5]

Factors influencing social preferences

Results of the LMMs suggest that variation in females' social preferences were not strongly influenced by the stable dyadic attributes that were measured. Association indices were higher among females who shared longer periods of lactational overlap (GLMM, est ± SE= 0.04 ± 0.02, P = 0.02, see Table 6). However, none of the test predictors explained variation in preferences for grooming (Likelihood ratio test, X_5= 6.1, P = 0.30) or for the measure of behavioral coordination from the FA (Likelihood ratio test, X_5= 5.3, P = 0.40). Results were similar when evaluating proximity preferences (Likelihood ratio test, X_5= 5.4, P = 0.36) and GG-rubbing preferences (Likelihood ratio test, X_5= 2.0, P = 0.85) as separate responses. Although dyadic co-residency time did not have the predicted positive effects on patterns of association or affiliation, it did predict aggression ($F_{4,18} = 16.58$, $P = 0.002$). Aggression was highest among females who had resided together in the community for shorter periods of time (GLMM, est ± SE= 0.28 ± 0.05, $P < 0.001$, see Table 6 and Figure 3). [Insert Table 6 and Figure 3].

Influence of social preferences on the likelihood of cooperation

There were N = 31 cases of female dyadic coalitionary aggression where the identities of the aggressor and her coalition partner were confirmed, involving 28 % (N = 22) of female dyads. The occurrence of dyadic coalitionary support was not influenced by variation in grooming preferences, extent of behavioral coordination or aggression indices (Likelihood ratio test, $X_3 = 0.88$, $P = 0.83$). Similar results were obtained when testing proximity and GG-rubbing preferences as separate predictors in the model (Likelihood ratio test, $X_4 = 1.42$, $P = 0.84$).

Food sharing was observed on N = 43 different days, during which food transfers of fruit, honey or meat occurred between one or more female food possessors and other females. Food sharing was observed between 58 % (N = 45) of female dyads. The likelihood that dyads engaged in food sharing during the study period was influenced by the test predictors (Likelihood ratio test, $X_3 = 7.9$, $P = 0.047$), due to an increased likelihood of food sharing among dyads with higher measures of behavioral coordination, based on the results of the FA (GLMM, est ± SE = 0.98 ± 0.45, P = 0.03, see Table 7 and Figure 4). Variation in grooming and aggression preferences did not influence the likelihood that dyads shared food (see Table 7). When we ran models separately for each year, the composite measure of behavioral coordination had a similar effect on the likelihood of food sharing in year one (est ± SE = 1.45 ± 0.32, P = 0.01) and year three (est ± SE = 0.89 ± 0.51, P = 0.08), suggesting that shifts in the extent of dyadic behavioral coordination between years influence annual patterns of dyadic food sharing. The year two model was not stable, due to too few food sharing episodes. When proximity and GG-rubbing preferences were run separately in the model, only proximity preferences predicted food sharing (GLMM, est ± SE= 0.93 ± 0.40, *P* = 0.02). Comparison of the AIC values between models suggests that the model containing the combined measure of behavioral coordination provides a better fit to the data in comparison with the model where each predictor is tested separately (Δ AIC = 3). [Insert Table 7 and Figure 4].

DISCUSSION

Our results suggest that female bonobos at LuiKotale use distinct social behaviors to maintain different types of more and less differentiated relationships. Consistent with findings from other study sites (Lomako: Hohmann & Fruth, 2002;

Waller, 2011; Wamba: Furuichi, 2009; Hashimoto & Furuichi, 2015, see Table 1), resident females from the Bompusa community were rarely observed in parties without other adult females present. However, there was no evidence that specific dyads either sought each other out or avoided associating together in sub-groups during fission events, when we predicted that females would make decisions about association based on social preferences. The lack of evidence for long-term preferred partners for party association is consistent with previous research in bonobos (Hohmann, Gerloff, Tautz, & Fruth, 1999), and similar to evidence from female spider monkeys, who maintain high overall levels of association in sub-groups, but with no evidence for selectivity in choice of specific female partners (Ramos-Fernández, Boyer, Aureli, & Vick, 2009). These results contrast with evidence for strong and stable dyadic preferences for party association among both western and eastern female chimpanzees (Langergraber et al., 2009; Lehmann & Boesch, 2009), which are sufficient to differentiate female social relationships at some study sites (Langergraber et al., 2009).

Although females did not have strong preferences for association partners, lactating females were more likely to remain together during fissions, which may reflect their similar energetic constraints that make associating in large parties more costly (Wrangham 2000). By associating together, lactating females may also gain additional benefits through enhanced socialisation opportunities for immature offspring. Female chimpanzees at Gombe also prefer to associate in parties with other females who have similarly-aged offspring (Foerster et al., 2015), and for male chimpanzees, having more gregarious mothers early in life has a positive influence on their fitness later in life (Williams et al., 2002).

In contrast with the lack of preferred social partners during fission events, females did have preferred partners for other social behaviors. This was especially evident for grooming based on the more right-skewed distribution, greater variance in scores and larger number of dyads with preference scores significantly above or below expected values in comparison with the other preference indices (see Fig. 1 and Table 3). In addition, only grooming preferences were stable between consecutive years. That grooming preferences were stronger and more stable relative to the other social measures is not surprising given the higher opportunity costs associated with grooming (Dunbar, 2012). Grooming requires greater time investment than GG-rubbing, and typically occurs with one partner at a time, unlike maintaining close proximity, which can be achieved with several partners simultaneously. Thirteen females, or 16.7% of dyads, had stable, significantly higher than expected grooming preference scores, which corresponds closely with the proportion of female dyads identified as being preferred social partners across several chimpanzee communities, based on stable associations in sub-groups at significantly higher than expected levels (14 % of female dyads at Tai: Lehmann & Boesch, 2009; 17 % of female dyads at Ngogo: Langergraber et al. 2009). Although genetic analyses confirmed maternal-relatedness among 11.5% (N = 13) of mature female dyads, none of these dyads exhibited preferential grooming relationships (see Fig. 2). Our results are strikingly similar to a previous study from the E1 community of Wamba, which also identified 11% (5 of 45) of dyads as likely maternal relatives, based on estimates of genetic relatedness, and found no indication that putative female relatives had higher indices of proximity or grooming compared with unrelated females (Hashimoto, Takenaka and Furuichi, 1996). [Insert Figure 2].

In addition to maintaining stable, preferred grooming relationships, Bompusa females also had preferred partners for proximity, GG-rubbing and aggression that fluctuated across years. That patterns of overall aggression were lower among residents who had been in the community for longer suggests that social integration may occur over many years, during which females develop strategies to reduce conflict. However, variation among females in affiliative behaviors such as proximity, grooming and GG-rubbing was not linked to any stable female attributes and may rather reflect strategic, short-term investments.

The results of the FA and GLMMs help to explain why female bonobos may maintain different types of social relationships that vary in their behavioral expression and stability. The FA reduced the data to one factor, explained primarily by variation across dyads in their preferences to remain in close proximity, and to engage in a socio-sexual behavior that has been linked to signaling social tolerance and mitigating potential social conflicts. Previous research indicates that GG-rubbing increases when feeding on potentially monopolizable foods (Hohmann & Fruth, 2000) and engaging in GG-rubbing increases the likelihood that partners will feed in close proximity afterwards (Douglas & Moscovice, 2015). If females are motivated to stay in close proximity to others with whom they may not be strong affiliates in other contexts, then GG-rubbing may provide a means for these females to coordinate their behavior while avoiding conflicts.

The ability to maintain high levels of behavioral coordination with a large network of social partners may be especially adaptive for female bonobos given the potential for fluctuations in female presence on a daily and more long-term basis. Flexible shifting of investment in social partners also occurs in other fission-fusion species and may be used strategically to achieve various forms of polyadic cooperation, such as hunting and territorial defense among philopatric male chimpanzees (Langergraber, Mitani, & Vigilant, 2007) and coordinated herding of females by fluctuating coalition partners within larger “super-alliances” among philopatric male dolphins (Connor & Krützen, 2015). Such behavioral coordination may help females to influence group travel (Furuichi 2012), coordinate entry into feeding locations and subsequently out-compete males for access to preferred feeding sites (White & Wood, 2007) and food resources (Hohmann & Fruth, 1996). Such cooperation may represent mutualisms if all females involved benefit through reduced competition from males for access to food, and through reduced likelihood of male harrassment while feeding. In addition, our results suggest that females who maintain higher levels of behavioral coordination are more likely to share potentially monopolizeable foods. In this context, food sharing may also represent a form of mutualism, as suggested by Fruth and Hohmann (2002), based on evidence that female food possessors at Lomako who share with a subset of supplicants retain possession of food items for longer than females who do not share, possibly due to help from supplicants in co-defending the food. In addition, food sharing may provide a means to reinforce tolerant relationships among non-kin. This is supported by evidence from Goldstone and colleagues (2015) that food begging at LuiKotale was most frequently initiated by younger females and directed at older female food possessors, and may be used as a social tool to assess relationships. Goldstone and colleagues (2015) found no relationship between the likelihood of receiving food and short-term measures of grooming or GG-rubbing between partners, although GG-rubbing was related to increases in begging behavior. During our study, only 50% (N = 8) of females with preferred grooming relationships also shared food, and this explained only a small proportion of all food sharing dyads. In addition, GG-rubbing preferences did not influence food sharing patterns when measured independently of proximity preferences. Using the FA, we identified a composite measure of proximity and grooming preferences that helped to explain the occurrence of food sharing among a relatively large proportion of female dyads over a three year period. In addition to maintaining stable grooming relationships, having flexibility to coordinate behavior with different partners under varied social contexts may help unrelated females to maintain high levels of mutually-beneficial cooperation.

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LITERATURE CITED

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1-48. doi:10.18637/jss.v067.i01.

Budaev, S. V. (2010). Using principal components and factor analysis in animal behavior research: caveats and guidelines. *Ethology*, *116*(5), 472–480.

Candiotti, A., Coye, C., Ouattara, K., Petit, E. J., Vallet, D., Zuberbühler, K., & Lemasson, A. (2015). Female Bonds and Kinship in Forest Guenons. *International Journal of Primatology*, *36*(2), 332–352. http://doi.org/10.1007/s10764-015-9829-1

Chajewski, M. (2009). rela: Scale item analysis. R package version 4.1.

Clay, Z., Furuichi, T., & De Waal, F. B. M. (2016). Obstacles and catalysts to peaceful coexistence in chimpanzees and bonobos. *Behaviour*. http://doi.org/10.1163/1568539X-00003335

Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*(7269), 51–7. http://doi.org/10.1038/nature08366

Clutton-Brock, T., & Janson, C. (2012). Primate socioecology at the crossroads: Past, present, and future. *Evolutionary Anthropology*, *21*(4), 136–150. http://doi.org/10.1002/evan.21316

Clutton-Brock, T. H., & Lukas, D. (2012). The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, *21*(3), 472–492. http://doi.org/10.1111/j.1365-294X.2011.05232.x

Connor, R. C., & Krützen, M. (2015). Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Animal Behavior*, *103*, 223–235.

Cross, P. C., Lloyd-Smith, J. O., & Getz, W. M. (2005). Disentangling association patterns in fission–fusion societies using African buffalo as an example. *Animal Behavior*, *69*(2), 499–506. http://doi.org/10.1016/j.anbehav.2004.08.006

Douglas, P. H., Ngonga Ngomo, A. C., Hohmann, G. (*in press*). A Novel Approach for Dominance Assessment in Gregarious Species: ADAGIO. *Animal Behaviour*.

Douglas, P. H., & Moscovice, L. R. (2015). Pointing and pantomime in wild apes? Female bonobos use referential and iconic gestures to request genito-genital rubbing. *Scientific Reports*, *5*, 13999.

Dunbar, R. I. M. (2012). Bridging the bonding gap: the transition from primates to humans. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*(1597),1837–1846.

Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behavior*, *73*, 501–512.

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: partner preferences among adult female chimpanzees. *Animal Behavior*, *105*, 139–152.

Fox, J. and Weisberg, S. (2011). An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Fraser, O. N., Schino, G., & Aureli, F. (2008). Components of relationship quality in chimpanzees. *Ethology*, *114*(9), 834–843.

Fruth B, Hohmann G (2002) How bonobos handle hunts and harvests: why share food? In: Boesch C, Hohmann G, Marchant L (eds) Behavioral diversity in chimpanzees and bonobos. Cambridge Univ Press, Cambridge, pp 231–243.

Fruth, B., & Hohmann, G. (2006). Social grease for females? Same-sex genital contacts in wild bonobos. In S. V. Sommer & P. L. Vasey (Eds.), *Homosexual Behavior in Animals: An evolutionary perspective* (pp. 294–315). New York: Cambridge Univ Press.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, *18*(6), 855–875.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. *Primates*, *50*(3), 197–209.

Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology*, *20*(4), 131–142. http://doi.org/10.1002/evan.20308

Gerloff, U., Hartung, B., Fruth, B., Hohmann, G., & Tautz, D. (1999). Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1424), 1189–1195.

Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, *62*(11), 1831–1842.

Godde, S., Humbert, L., Côté, S. D., Réale, D., & Whitehead, H. (2013). Correcting for the impact of gregariousness in social network analyses. *Animal Behavior*, *85*(3), 553–558. http://doi.org/10.1016/j.anbehav.2012.12.010

Goldstone, L. G., Sommer, V., Nurmi, N., Stephens, C., & Fruth, B. (2016). Food begging and sharing in wild bonobos (*Pan paniscus*): assessing relationship quality? *Primates*, *57*(3), 367–376. http://doi.org/10.1007/s10329-016-0522-6

Hashimoto, C., Takenaka, O., & Furuichi, T. (1996). Matrilineal kin relationship and social behavior of wild bonobos (Pan paniscus): Sequencing the D-loop region of mitochondrial DNA. *Primates*, *37*(3), 305–318. http://doi.org/10.1007/BF02381862

Hohmann, G., & Fruth, B. (1996). Food sharing and status in unprovisioned bonobos. In P. Wiessner & W. Schiefenhoevel (Eds.), *Food and the Status*

Quest: Interdisciplinary perspectives (Vols. 1–WI 021139, pp. 47–67). Providence: Berghahn Books.

Hohmann, G., & Fruth, B. (2000). Use and function of genital contacts among female bonobos. *Animal Behavior*, *60*(1), 107–120.

Hohmann, G., & Fruth, B. (2002). Dynamics in social organization of bonobos (*Pan paniscus*). In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioral Diversity in Chimpanzees and Bonobos* (pp. 138–150). New York: Cambridge Univ Press.

Hohmann, G., & Fruth, B. (2003a). Intra-and inter-sexual aggression by bonobos in the context of mating. *Behavior*, *140*(11), 1389–1414.

Hohmann, G., & Fruth, B. (2003b). Lui Kotal - A new site for field research on bonobos in the Salonga National Park. *Pan Africa News*, *10(2)*, 25–27.

Hohmann, G., Gerloff, U., Tautz, D., & Fruth, B. (1999). Social bonds and genetic ties: Kinship, association and affiliation in a community of bonobos (*Pan paniscus*). *Behavior*, *136*(9), 1219–1235.

Idani, G. (1991). Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatologica*, *57*(2), 83–95.

Isbell, L. A., & Young, T. P. (2002). Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behavior*, *139*(2), 177–202.

Jaeggi, A. V., Boose, K. J., White, F. J., & Gurven, M. (2016). Obstacles and catalysts of cooperation in humans, bonobos, and chimpanzees: behavioural reaction norms can help explain variation in sex roles, inequality, war and peace. *Brill*. http://doi.org/10.1163/1568539X-00003347

Kalbitz, J., Ostner, J., & Schülke, O. (2016). Strong, equitable and long-term social bonds in the dispersing sex in Assamese macaques. *Animal Behavior*, *113*, 13–22. http://doi.org/10.1016/j.anbehav.2015.11.005

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, *23*(4), 759–783.

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences, USA*, *104*(19), 7786–7790.

Langergraber, K. E., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840–851.

De Lathouwers, M. D. & Elsacker, L. V. (2006). Comparing infant and juvenile behaviour in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): a preliminary study. *Primates*, *47*(4), 287–293. http://doi.org/10.1007/s10329-006-0179-7.

Lee, P.C. and Strier, K.B. Complexities of understanding female dispersal in primates. In Furuichi, T., Aureli, F. and Yamagiwa, J. (eds): Dispersing Primate Females. Springer, Japan, 215-230.

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*.

Animal Behavior, *77*(2), 377–387.

Mulavwa, M., Furuichi, T., Yangozene, K., Motema-salo, B., Idani, G., Ihobe, H., … Mwanza, N. (2008). Seasonal Changes in Fruit Production and Party Size of Bonobos at Wamba. *The Bonobos: Behavior, Ecology & Conservation*, 121–135. http://doi.org/10.1007/978-0-387-74787-3_8

Nsubuga, A. M., Robbins, M. M., Roeder, A. D., Morin, P. A., Boesch, C., & Vigilant, L. (2004). Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. *Molecular Ecology*, 13(7), 2089-2094.

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B.,…Wagner, H. (2015). vegan: Community Ecology Package. R package version 2.3-2. http://CRAN.R-project.org/package=vegan

Oelze, V. M. (2015). Reconstructing temporal variation in great ape and other primate diets: A methodological framework for isotope analyses in hair. *American Journal of Primatology*, http://doi.org/10.1002/ajp.22497

Parish, A. R. (1996). Female relationships in bonobos (*Pan paniscus*): Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Human Nature*, *7*(1), 61–96.

Ramos-Fernández, G., Boyer, D., Aureli, F., & Vick, L. G. (2009). Association networks in spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology*, *63*(7), 999–1013. http://doi.org/10.1007/s00265-009-0719-4

Ryu, H., & Hill, David A.Furuichi, T. (2015). Prolonged maximal sexual swelling in wild bonobos facilitates affiliative interactions between females. *Behaviour*, *152*(3–4), 285–311. http://doi.org/10.1163/1568539X-00003212

Sakamaki, T. (2013). Social grooming among wild bonobos (*Pan paniscus*) at Wamba in the Luo Scientific Reserve, DR Congo, with special reference to the formation of grooming gatherings. *Primates*, *54*(4), 349–359. http://doi.org/10.1007/s10329-013-0354-6

Silk, J. B. (2009). Nepotistic cooperation in non-human primate groups. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1533), 3243–3254.

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*). I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, *61*(2), 183–195.

Slater, K. Y., Schaffner, C. M., & Aureli, F. (2009). Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of Primatology*, *71*(1), 21–29.

Städele, V., & Vigilant, L. (2016). Strategies for determining kinship in wild populations using genetic data (advance online). Ecology and Evolution.

Sterck, E. H., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291–309.

Stevens, J. M. G., de Groot, E. & Staes, N. (2015). Relationship quality in captive bonobo groups. *Behavior*, *152*(3–4), 259–283. http://doi.org/10.1163/1568539X-00003259

Strier, K. B. (1994). Myth of the typical primate. *American Journal of Physical Anthropology*, *37*(S19), 233–271.

Surbeck, M., & Hohmann, G. (2013). Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behavioral Ecology and Sociobiology*, *67*, 1767–1780.

Tokuyama, N., & Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour*, *119*, 27–35.

Vigilant, L., Pennington, R., Harpending, H., Kocher, T.D., & Wilson, A. C. (1989) Mitochondrial DNA sequences in single hairs from a southern African population*. Proceedings of the National Academy of Sciences USA,* 86*,* 9350–9354.

Villesen, P. (2007), *FaBox: an online toolbox for fasta sequences*, *Molecular Ecology Notes* 7 (6), 965–968. doi:10.1111/j.1471-8286.2007.01821.x

Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behavior*, *85*(6), 1303–1313.

Waller, M. T. (2011). *The ranging behavior of bonobos in the Lomako Forest*. Dissertation Thesis, University of Oregon. Retrieved from https://scholarsbank.uoregon.edu/xmlui/handle/1794/11648

White, F. J. 1998. Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. International Journal of Primatology 47: 1013-1027.

White, F. J. and M. A. Burgman. 1990. Social organization of the pygmy chimpanzee (Pan paniscus): multivariate analysis of intracommunity associations. American Journal of Physical Anthropology 83: 193-201.

White, F. J. and C. A. Chapman. 1994. Contrasting chimpanzees and pygmy chimpanzees: nearest neighbor distances and choices. Folia Primatologica 63; 181-191.

White, F. J., & Wood, K. D. (2007). Female feeding priority in bonobos, *Pan paniscus*, and the question of female dominance. *American Journal of Primatology*, *69*(8), 837–850.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behavior*, *75*(3), 262–300.

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: P. M. Kappeler (Ed.), *Primate Males: Causes and Consequences of Variation in Group Composition*. (pp. 248-258). Cambridge University Press.

Figure 1. Distributions of dyadic preference indices among N = 78 female dyads for: staying in close proximity, grooming and GG-rubbing. Lighter shading indicates the preference scores for the N = 9 dyads that are maternally related based on genetic analyses.

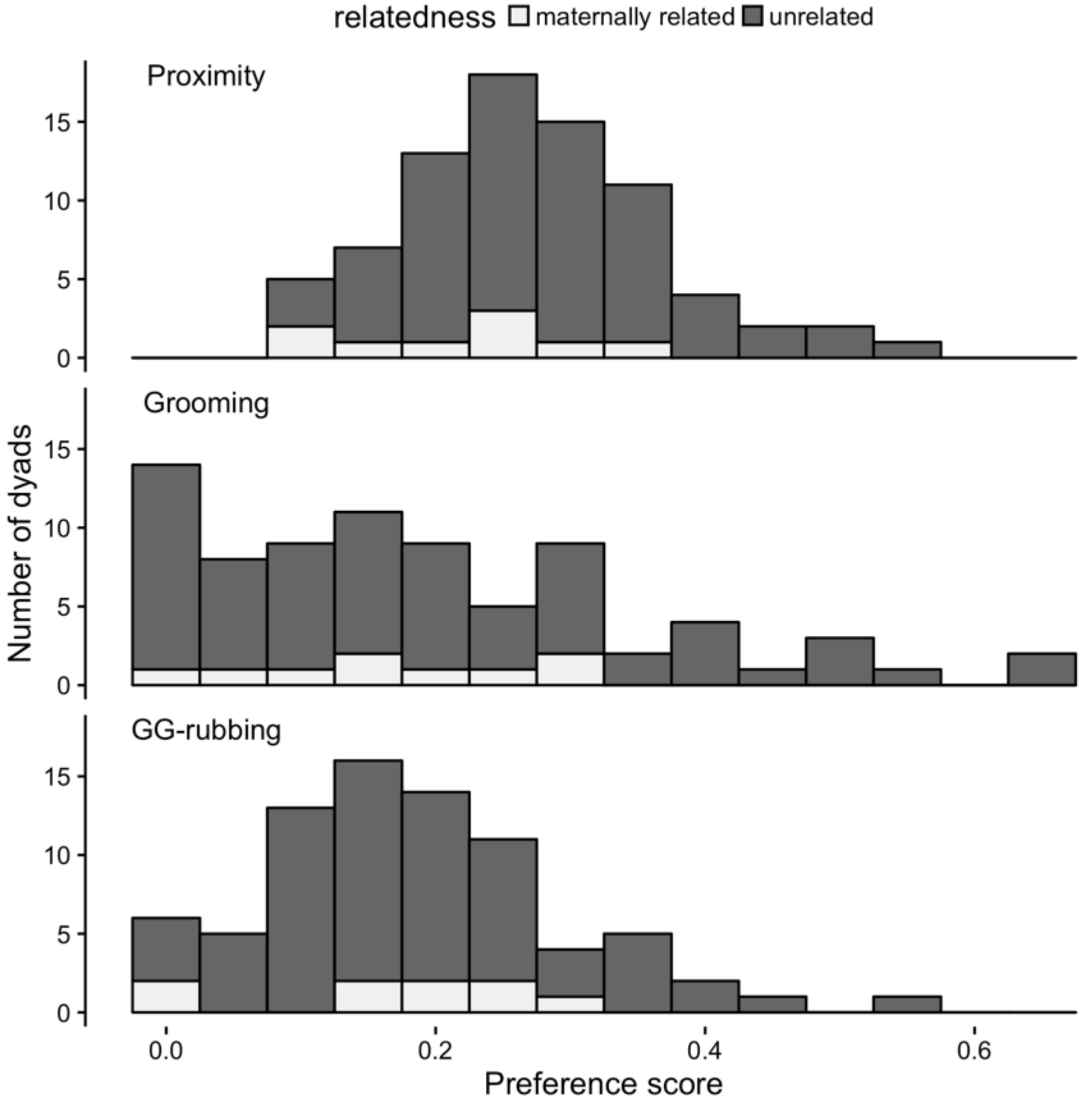

Figure 2. Matrix summarizing results of genetic analyses and permutation tests indicating preferred social partners for proximity (PROX), grooming (GR) and GG-rubbing (GG). Shaded boxes indicate putative maternal relatives, based on identification of shared mtDNA haplotypes. Dyads with proximity, grooming and/or GG-rubbing preferences that are significantly higher than expected are indicated.

	Ir	Lu	Ma	Na	Ol	Pa	Po	Ri	Su	Um	Wi	Zo
Gw					GG	▨	▨			▨		
Ir				▨	PROX+GR							
Lu			GR	GR		GR		▨		PROX+GR		
Ma				GR		PROX+GR					GR	
Na					GR		PROX	GR+GG			PROX+GG	PROX
Ol						PROX	GR	PROX	PROX			
Pa							▨			▨		
Po									GR+GG	▨	GR+GG	GG
Ri												
Su												▨
Um												PROX
Wi												

Figure 3. Relationship between the aggression index and dyadic co-residency time (short= 1–4 years, medium= 4–8 years, long= >8 years). Box plots indicate medians and 25–75% inter-quartile ranges. Darker circles indicate a larger number of overlapping scores. For full model results refer to Table XX.

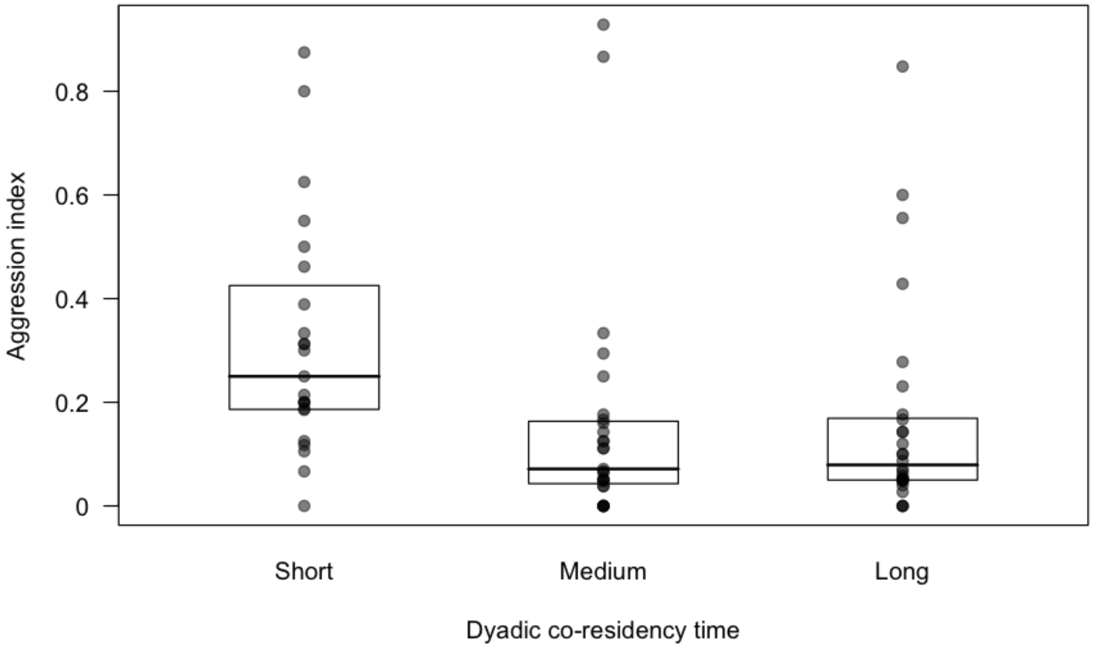

Figure 4. Results of the GLMM modeling the probability of food sharing among N = 78 female dyads in relation to their factor scores for the composite measure of behavioral coordination. Larger circles indicate a larger number of dyads contributing to the observed scores. The regression line indicates the expected probabilities of food sharing from the model. For full model results refer to Table 5.