**Predictability in the social relationships of sooty mangabeys and chimpanzees**

**Alexander Mielke1,2,#, Anna Preis1,2, Liran Samuni1,2, Jan F. Gogarten2,3,4, Jack Lester1, Catherine Crockford1,2,a, Roman M. Wittig1,2,a,#**

1 Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany

2 Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, Abidjan, Côte d'Ivoire

3 McGill University, Department of Biology, Montreal, Canada

4 Robert Koch Institute, P3: “Epidemiology of Highly Pathogenic Microorganisms”, Berlin, Germany

a C.C. and R.M.W. contributed equally to this work.

**#correspondence: alexander.mielke@eva.mpg.de, wittig@eva.mpg.de**

**ABSTRACT**

The social complexity of animal groups can be defined by how much information individuals need to predict others’ actions and reactions in social interactions. Individuals can use different sources of information to predict the behaviour of others. A standardised set of measures to capture predictability from the individual’s perspective would facilitate the comparison of social complexity between species. We present three measures for quantifying the predictability of relationships in social groups. Predictability can be considered high if interaction distributions are highly consistent, are based on easily assessable parameters (such as kinship, rank, sex, or association), or if dyads can be classified into repeatable social relationship types. We applied these three metrics to Western chimpanzees (*Pan troglodytes verus*) and sooty mangabeys (*Cercocebus atys atys*) living in Taï National Park, Côte d’Ivoire. One of our predictability measures, quantifying consistency, provides a useful tool to identify interaction types where low data density potentially influences analytical outcomes. In addition, predictability differed between and within communities and species. Chimpanzee interaction distributions were overall less consistent than mangabey interaction distributions, and directed interactions showed more consistent distributions than spatial proximity measures. The impact of the easily assessable parameters varied within species, but showed few species differences. Most male chimpanzee dyads were characterised by ambivalent relationships with high levels of grooming and aggression, potentially making relationships highly unpredictable; this relationship type was absent in both mangabeys and female chimpanzees. Our results suggest that the predictability of social relationships was lower in chimpanzees than mangabeys, indicating more complexity in chimpanzee sociality compared to mangabeys, but that social complexity did not vary only along one dimension. Thus the multivariate approach chosen here can form the basis for more comprehensive comparisons of social complexity within and between animal species.

Key Words: Chimpanzee, Sooty Mangabey, Social Relationships, Complexity, Predictability, Interactions

**INTRODUCTION**

Animals living in permanent social groups have to decide when and how to interact with group members and their ability to make the correct choice has potential fitness implications. Presumably, such decisions are informed by previous interactions with group members (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Schino & Aureli, 2017; Wittig, Crockford, Langergraber, & Zuberbühler, 2014), the attributes of potential partners (Hirsch, Prange, Hauver, & Gehrt, 2013; Madden, Nielsen, & Clutton-Brock, 2012; Naud et al., 2016), the local availability of resources (Miller et al., 2014), and the presence of alternative partners (Gumert, 2007; Kaburu & Newton-Fisher, 2016; Mielke et al., 2018). It has long been hypothesised that the evolution of cognitive skills is a response to the selection pressure imposed by the complexity of the social environment (Byrne & Whiten, 1989; Humphrey, 1976). This hypothesis has mostly been presented with the rationale that animals in more “complex” social systems must integrate more information about group members and their behaviour to out-compete others and therefore to increase their own fitness (Byrne & Whiten, 1989; Dunbar, 1993).

Social complexity has often been operationalised by the number of independent elements in a system (McShea, 1996), resulting in one-dimensional complexity measures based on structural properties of communities such as group size (Dunbar & Shultz, 2007). However, structurally complex social organisation can emerge as a property of social networks without underlying complex individual decision-making (Anderson & McShea, 2001; Barrett, Henzi, & Rendall, 2007; Ramos-Fernández, Boyer, & Gómez, 2006), so structural measures are possibly poor predictors for the evolution of cognitive skills in a species. Alternatively, others have defined complexity as the number of rules necessary to successfully predict future states of a system (Flack, 2012; Sambrook & Whiten, 1997). This *relational complexity* (Lukas & Clutton-Brock, 2018) in social groups can be seen as the amount of information necessary for an individual to predict interaction patterns of group members (Connor, 2007; Halford, Wilson, & Phillips, 1998; Whiten, 2000). Following this definition, complexity is low if a small set of rules constrains interaction patterns, or if no rules exist and interactions are distributed randomly (Sambrook & Whiten, 1997). Relational complexity is high if decisions are rule-based, but the number of rules to replicate the pattern is high (Sambrook & Whiten, 1997).

Comparable measures of how predictable interactions are from the perspective of individuals living in a community, i.e. their relational complexity, could allow us to link aspects of an individual’s social life to the evolution of complex decision-making abilities and cognition more directly than structural measures can (Dunbar & Shultz, 2010). The continuing appeal of structural measures of complexity is their comparability across animal communities when available datasets are small. However, for many animal species, detailed, long-term, individual-level behavioural data exist, emphasising the multifaceted nature of the social relationships of individuals, i.e., the entirety of their interactions with each other (Hinde, 1976). A standardised set of measures that captures the predictability of social interactions could enable us to identify contexts where flexible decision-making might play a role, and provide a toolbox to describe social groups in a replicable and comprehensive manner. It could also help us test whether structural descriptions, like the extent of fission-fusion dynamics (Aureli et al., 2008; Ramos-Fernandez et al., 2018), actually correlate with complexity from the perspective of an individual. Here, we combine three aspects of the predictability of interaction patterns to understand how relationships in animal communities are structured.

First, relationships are more predictable if partner choice is highly *consistent* over repeated interactions (Kalbitz, Ostner, & Schülke, 2016; Koski, de Vries, van de Kraats, & Sterck, 2012; Moscovice et al., 2017; Silk, Alberts, & Altmann, 2006) and observing a subset of interactions allows individuals to accurately predict the future distribution of the same interaction type (Whiten, 2000). An example of this are steep linear dominance hierarchies, in which observing a single social interaction between two individuals contains enough information to predict future contest (Guillermo Paz-Y-Miño, Bond, Kamil, & Balda, 2004; Oliveira, McGregor, & Latruffe, 1998; Sánchez-Tójar, Schroeder, & Farine, 2017). Low consistency can be the result of an unpredictable distribution of social interactions or of frequent changes in relationships over time, both indicating an increased need for cognitive flexibility (Barrett, Gaynor, & Henzi, 2002).

Second, relationships are more predictable when interaction patterns are based on *stable and easily assessable parameters* of the partner, such as kinship (Hirsch, Stanton, & Maldonado, 2012), sex (Foerster et al., 2015; Lehmann & Boesch, 2008), spatial association (Hemelrijk, 1999; Puga-Gonzalez, Hildenbrandt, & Hemelrijk, 2009), or dominance rank (Schino, 2001). Their values can be either identified immediately (whether other individuals are present or not), are fixed (sex, kinship), or are known to be recognised easily by social animals (dominance rank). These parameters have been shown to influence relationships across a large variety of species (e.g., guinea baboons: Goffe, Zinner, & Fischer, 2016; hamadryas baboons: Leinfelder, De Vries, Deleu, & Nelissen, 2001; dusky dolphins: Pearson, 2009; spotted hyeans: Smith, Memenis, & Holekamp, 2007; geladas: Tinsley Johnson, Snyder-Mackler, Beehner, & Bergman, 2014; yellow-bellied marmots: Wey & Blumstein, 2010).

Third, relationships are assumed to be more predictable if they can be categorised into a small number of repeatable *relationship types* (Bergman & Beehner, 2015; Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017; Whitehead, 2008a), such as male-female “friendships” in chacma baboons (Palombit, Seyfarth, & Cheney, 1997) or “affiliates” in bottlenose dolphins (Gero, Bejder, Whitehead, Mann, & Connor, 2005). Distinct relationships would go hand in hand with increased network overlap, if individuals show the same partner preference across interaction types (Barrett, Henzi, & Lusseau, 2012; Chan, Fushing, Beisner, & McCowan, 2013; Lea, Blumstein, Wey, & Martin, 2010; Lehmann, Andrews, & Dunbar, 2010; Madden, Drewe, Pearce, & Clutton-Brock, 2009). Rather than keeping track of all interactions they have with each group member, individuals could categorise relationships and interact the same way with all members of a category (Bergman & Beehner, 2015). For example, four different relationship types (frequent affiliative dyads, ambivalent dyads, rare affiliative dyads, rare agonistic dyads) have been identified in Barbary macaques using cluster analysis (Fischer et al., 2017). A social system is simple if a small number of clearly distinct relationship types exist; more relationship types or an inability to assign clear categories indicates higher complexity (Bergman & Beehner, 2015; Fischer et al., 2017).

We chose these three measures as they rely on information widely available to researchers studying social animals in captive or field settings, can be used for very different social interaction types, and capture many of the sources of species differences that have been hypothesised to exist in different social systems. While they will not cover all potential sources of unpredictability experienced by social animals, we see them as a good starting point for building up a standardised toolbox that can be widely applied to other species. Such a toolbox can provide a way to test whether species differences in structural measures (such as hierarchy steepness, fission-fusion dynamics, group size) actually translate into differences in the predictability of relationships from the standpoint of the individual. It would also provide a concise way of representing social groups and estimate their social complexity: often different interaction types and metrics for a study population are distributed over multiple publications using different methods. Developing one format to bundle information would allow researchers to describe their study system in a way that is readily comparable to existing datasets, similar to what has been attempted by creating the macaque social style scale (Thierry, Iwaniuk, & Pellis, 1999).

We test the applicability of these three metrics (consistency, easily assessable parameters, relationship types) as a standardised way to compare relational complexity across species. To show how they can be used to compare social groups with different structure and organisation, we apply them to data from two Western chimpanzee (*Pan troglodytes verus*) communities and one sooty mangabey (*Cercocebus atys atys*) community living sympatrically in the Taï National Park, Côte d’Ivoire (Mielke et al., 2017, 2018). We chose these two species as they represent two well-studied primate social systems: male philopatric species with high fission-fusion dynamics and female philopatric, matrilineal species with low fission-fusion dynamics, respectively. All involved communities are of similar size (40-60 individuals) and consist of multiple males and females that interact at high rates, but the rules underlying interaction patterns are expected to differ between species. We included two communities of chimpanzees to see whether interaction patterns are species-specific or if group-specific differences exist. Strong species differences in the three metrics of predictability could indicate species differences in the information processing necessary to navigate the social environment.

Sooty mangabeys here are a model for species with philopatric females who form linear, despotic, stable matrilineal hierarchies (Mielke et al., 2017; Range, 2006; Range & Noë, 2002). Limited rank changes between individuals were observed in this community during the study period for either sex (Mielke et al., 2018). Thus, all interaction types are predicted to show high consistency, as they should be influenced strongly by easily assessable parameters, especially kinship, dominance rank, and sex (Range & Noë, 2002). We predict clear relationship types, differentiating strong affiliative partners from agonistic dyads (especially males) and those dyads who rarely or never interact (Fischer et al., 2017).

Chimpanzees form male philopatric societies with stable linear hierarchies, but aggression in both communities studied here is frequently directed up as well as down the dominance hierarchy (Wittig & Boesch, 2003). In contrast to the mangabey community, we observed rank changes in both sexes in the study period (Mielke et al., 2018; Preis, Samuni, Deschner, Crockford, & Wittig, 2019). Maternal kinship is generally considered to only weakly influence relationships (Langergraber, Mitani, & Vigilant, 2007), and enduring social bonds between non-kin individuals exist (Langergraber, Mitani, & Vigilant, 2009; Mitani, 2009). Many aspects of chimpanzee life, like the impact of females on the social network (Lehmann & Boesch, 2008, 2009; Wittiger & Boesch, 2013), or the impact of rank on grooming patterns, differ between communities (Arnold & Whiten, 2003; Gomes, Mundry, & Boesch, 2009; Kaburu & Newton-Fisher, 2015). Chimpanzees show strong fission-fusion dynamics, with clearly separated subgroups forming over multiple days, indicating a strong connection between interaction distribution and spatial association. However, this could also lead to less consistent interaction patterns, as individuals select interaction partners out of changing subsets of the community. Enduring social bonds have been described for both sexes in chimpanzees (Foerster et al., 2015; Mitani, 2009), so at least some of the relationships of each individual are predicted to fall into clear relationship types.

**METHODS**

*Data Collection*

Behavioural data were collected in Taï National Park, Côte d’Ivoire (Boesch & Boesch-Achermann, 2000) from October 2013 to July 2015 for the chimpanzees and January 2014 to September 2015 for the mangabeys, using half- and full-day continuous focal animal sampling (Altmann, 1974) for the chimpanzees, and half-day and one-hour focal animal sampling for the mangabeys. We created interaction patterns for the entire study period rather than cutting it into smaller time periods, as it was not clear which impact data density would have on the robustness of measures for the shortened segments (Whitehead, 2008b). Trained observers (AM, JFG, AP, LS) and field assistants recorded all social interactions of adult male and female chimpanzees (above 12 years of age) in the “South” (AM, AP, LS) and “East” (AP, LS) communities and adult (above 5 years) sooty mangabeys (AM, JFG). This resulted in 6441h of focal observations in South community, 5668h for East community, and 2259h for the mangabey community. We included adult individuals of both sexes in all three communities for whom sufficient focal data (at least 50 social interactions observed as focal individual) were available and who were present for at least 80% of the study period (South: 5 males, 7 females; East: 5 males, 7 females; mangabeys: 6 males, 17 females). For individuals with fewer interactions in the dataset, the error around interaction rates can be considered too large and results unreliable (Whitehead, 2008b). Based on these criteria, we had to exclude 9 adult females in the two chimpanzee communities (4 females in East, 5 in South) who migrated into the community during the study period or were not sufficiently habituated for focal follow, and 3 adult mangabey females who disappeared over the course of the study. All non-adult group members in all communities were also excluded due to insufficient focal follow data in the study period, despite the impact they probably would have on all presented measures (Fedurek & Lehmann, 2017). We chose to exclude individuals nevertheless because including individuals who were not followed regularly would make their interactions patterns unreliable. All variables were calculated for the entire sampling period. We conducted microsatellite analysis to establish adult mother-offspring pairs in the mangabey community (see Supplementary), to add to the known kinship ties in South community. East community does not have any known adult kin dyads, so kin was not included as a predictor in that community.

Dominance ranks in all communities were calculated using a modification of the Elo rating method (Foerster et al., 2016, see Mielke et al., 2017 for details). Ordinal ranks were standardised daily between 0 and 1, and each individual was assigned its average rank for the time period in question. We used the average daily Elo rather than the David’s Score as the two perform equally well when ranks are stable (Douglas, Ngonga Ngomo, & Hohmann, 2017), but the Elo retains more information if rank changes do occur. Mangabey ranks only changed when individuals migrated or died, while both male and female chimpanzees showed rank challenges in the study period (Mielke, Crockford, & Wittig, in press). All described analyses were conducted in R 3.5.1 (R Development Team 2017).

From the behavioural data, we extracted the duration of grooming sent and received, resting or foraging in less than 1m distance from the partner (“body contact”: used as a continuous measure with duration in the chimpanzees and an event variable in the mangabeys), resting or foraging as nearest neighbour between 1m and 3m distance (“proximity”), and both contact and noncontact aggressive interactions with one clear recipient (Preis et al., 2018). For the chimpanzee communities, we included food sharing (Samuni et al., 2018), which was not regularly observed in the mangabeys. We included highly predictable pant grunt vocalisations in the chimpanzees and supplants in the mangabeys to assess whether the consistency measure and the assessable parameter measure accurately capture the rules underlying distributions. Both these interaction types are known to be highly stable and linear, and therefore used to create the dominance ranks, so we predict that they have higher explained variance and consistency than the other interaction types. Mutual interactions were coded as interaction given and received. We treated body contact and proximity as interaction types with the assumption that both individuals have to show sufficient tolerance to allow the other one to remain close. Body contact and proximity were only counted if no other interaction took place within 5min before or after to ensure independence of data points. We included grooming, contact aggression, noncontact aggression, pant grunts/supplants, and food sharing as directional variables, with the distribution of interactions given from each individual to every other as outcome variable. For the two spatial proximity measures, data were considered non-directional and symmetrical. Interaction distributions were standardised by focal observation time, with observation time calculated by adding the total observation times of A and B for the study period. We did not standardise interaction rates by the observation time two individuals spent in the same party, as has been suggested for fission-fusion societies (Moscovice et al., 2017), because interaction rates would then be non-independent from association, one of our predictor variables. The same standardisation would not be possible for most long-term datasets in low fission-fusion species, reducing replicability with other studies. Spatial proximity and food sharing in the chimpanzees were collected by a subset of observers and were standardised based on the focal observation time provided by those observers. Aggregating party composition in chimpanzees and 15min scans of visible individuals in mangabeys into one-hour blocks, we calculated the simple ratio index of each dyad as a measure of how often they were in the same party compared to how many times they could have been in the same party, to represent their level of spatial association (Whitehead, 2008a).

*Ethical Note*

This study was purely observational with no manipulation of animals. Permissions to conduct the research were granted by the Ministry of Higher Education and Research in Ivory Coast (379/MESRS/GGRSIT/tm) and the Ministry of Water and Forest through the Office Ivorien des Parcs et Reserves. Methods were approved by the Ethikrat der Max-Planck-Gesellschaft (4.08.2014).

*Consistency*

Many behavioural studies depend on aggregated distributions of a particular interaction type over time, be it studies on social networks or cooperation in biological markets. Researchers can only observe a subset of interactions individuals are involved in, meaning that the “real” distribution of interactions is unknown and we have to assume that the collected data reflect it accurately (Farine & Strandburg-Peshkin, 2015; Kasper & Voelkl, 2009; Whitehead, 2008b). However, if data are sparse, the inclusion of many false zeros (i.e. dyadic values in the distribution that appear to be zero, but would not be with higher observation effort) increases the estimate's error and reduces the robustness of the resulting distribution (Lusseau, Whitehead, & Gero, 2008; Shizuka & Farine, 2016). Working with distributions which are not accurate representations of the underlying distribution can lead to misleading results (Davis, Crofoot, & Farine, 2018). This problem is aggravated when already sparse datasets are cut into shorter time intervals (e.g. 3 month blocks). What constitutes enough data can vary depending on how repeatable partner choice is (Sánchez-Tójar et al., 2017). The consistency measure we develop here can be used both to compare consistency across interaction types and species, and as a shortcut to identify interaction types for which the distribution might be based on too few data points. Consistency should be high if individuals regularly choose the same partners for the same interaction type, and observing the individual at one point in time allows for accurate predictions of their behaviour later. Low consistency can arise if individuals show weak partner preference or preference changes over time.

To quantify consistency, we used all the collected data for each interaction type and randomly assigned each observation day into one of two datasets of equal size (Sánchez-Tójar et al., 2017). We then calculated the distribution in each of the halves and calculated the non-parametric Spearman correlation between distributions. This allows us to estimate how well variation in one half predicts variation in the other. We repeated this procedure 100 times, with the median correlation coefficient constituting our measure of consistency for the full dataset. We present the impact of different group sizes, data densities, consistency of partner choice, and changes in underlying relationships in simulated datasets on our consistency measure in the Supplementary Material, and show how it can be used to compare consistency across communities of different sizes. As we show through data simulations, very inconsistent results (median correlation values between two halves of the dataset below 0.5) are usually due to very low data density, even if the underlying distribution is highly consistent. Thus, if interaction types are highly inconsistent, it is unclear whether the collected data is representative for the actual distribution in the population, and whether any of the subsequent results meaningfully describe the behaviour of individuals in a community. We therefore removed interaction types for which the median correlation value between halves was below 0.5.

As the overall correlation between halves was dependent on the data density and community size in the supplementary, we report a standardised version here: We repeated the consistency analysis using randomly selected subsets of the data. We randomly selected a start date and duration for the period following that date, and tested the consistency for this period for each interaction type, marking how many interactions per dyad this time period contained. This way, we can compare frequent and infrequent interaction types, or datasets of different sizes. As a standardised consistency measure, we report the median number of interactions per dyad that were sufficient to reach a cut-off correlation between halves of 0.5 for each interaction type. This measure is largely independent of data density and community size (see Supplementary), and produces an interpretable result: how many interactions between two group members does an individual have to observe to predict future interactions? Fewer interactions per dyads sufficient to reach this value and a smaller standard deviation of values indicate higher consistency and thus higher predictability, as individuals living in this community have to observe fewer interactions to reliably infer future behaviour of group members. Larger numbers of median interactions per dyad and a large standard deviation indicate that individuals would need to observe a large number of interactions to predict the patterns in their community. This can be either the case if partner choice is close to random for this interaction type, or if the choice patterns change throughout the study period.

*Impact of easily assessable parameters*

Stable and easily assessable parameters of potential partners structure who interacts with whom in a community. Primates can rapidly identify partner sex, dominance rank, and whether they are kin (Bergman, Beehner, Cheney, & Seyfarth, 2003; Borgeaud, van de Waal, & Bshary, 2013). Association patterns structure who can interact with whom and how often in a community (Hemelrijk, 1999). While the meaningful measure of association would be to assess for each decision made who is present or not (Mielke et al., 2018), this is not feasible when looking at interaction rates. Association rates are therefore the closes approximation we have for how often two individuals could have interacted with each other in the time period. Here, we are interested in two aspects: the amount of variation in interaction distribution these parameters explain together, and the relative importance of each parameter. To quantify the amount of variation these attributes explained, we fitted multiple Generalized Linear Mixed Models (GLMM; Baayen, Davidson, & Bates, 2008) with each interaction type (grooming, aggression, body contact, proximity, food sharing, pant grunts/supplants) in each community as the dependent variable. For the proximity measures, association, and grooming, we fitted LMMs with Gaussian error structure and identity link, using the dyadic interaction rates as the response variable. For aggression, food sharing, and pant grunts/supplants, we fitted GLMMs with Poisson error structure and log link, which better account for the count nature of the data (Dobson, 2002), and entered an offset term with the log-transformed observation time to account for differences in observation effort (Baayen et al., 2008). We fitted one model per community per behaviour, rather than comparing the communities directly in one global model, as this allows us to quantify the impact of each parameter and the explained variance in each community.

For directed social interaction types (grooming, aggression, food sharing, pant grunt/supplant), each dyad was represented twice, with each member of the dyad included once as sender and receiver. As fixed effects, we included the interaction of the sexes of both individuals (and also the respective main effects), the interaction of their z-standardized rank values (Schielzeth, 2010), their dyadic association index, and whether they were maternal kin or not. For non-directed social interaction types (body contact, proximity) each dyad was represented once, and we used a sex combination variable (male, female, mixed dyad), the absolute rank difference between the two individuals, the association index, and kinship as fixed effects. We included the identities of sender and receiver as random effects, and the identity of the dyad for directed interaction types. We included the random slopes for the association index and the rank of the respective partner in the random effects of sender and receiver (Schielzeth & Forstmeier, 2009). For non-directed interaction types, we included the random slope of the rank difference and association index in the random effects of sender and receiver. We did not include the correlation between random intercepts and random slopes.

To quantify how much variation of the response the entirety of fixed effects explained (Sambrook & Whiten, 1997), we calculated the R2 (Nakagawa & Schielzeth, 2013) as an effect size for the explained variance of the fixed effects portion of the full model using the function “r.squaredGLMM” from the R package “MuMIN” (Barton, 2018). We interpret the explained variance as the reliance of individuals on the predictors when deciding with whom to interact. We consider interaction distributions to be predicted strongly by the easily assessable parameters if the effect size R2 was above 0.6, and weakly predicted if R2 was below 0.2 (Cohen, 1988). To test the relative impact each of the parameters had on each behaviour, we used multimodel inference (Burnham & Anderson, 2002). The set of models we fitted for each interaction type in each community comprised all possible subsets of the easily assessable parameters of the full model. When the interaction of ranks was included into a submodel, the two main effects were also included. All submodels had the same random effect structure. The null model (excluding all easily assessable parameters) was included in the model set. We determined the AICc (Akaike’s Information Criterion, corrected for small sample sizes (Burnham & Anderson, 2002)) for each of the models and determined the Akaike weights and the 95% best model confidence set (Burnham & Anderson, 2002). If the null model was not in the confidence set, we calculated the summed Akaike weight per predictor. These values were compared to the expected sum of weights assuming that all models performed equally well (Wessling, Kühl, Mundry, Deschner, & Pruetz, 2018), to establish the rules underlying the interaction distribution for each interaction type.

The assignment of “sender” and “receiver” is problematic for the non-directed measures (body contact, proximity) as we do not have information about who initiated contact. The random effects structure still impacts the variance explained by the fixed effects, and we have to account for the impact of the identity of both individuals on the results to avoid pseudo-replication (Kulik, Muniz, Mundry, & Widdig, 2012). We used repeated random selection of either one or the other individual as “sender” or “receiver” to represent the dyad (Kulik et al., 2012; Mielke et al., 2017). We ran 1000 selections. For each selection, we fitted a Linear Mixed Model to estimate the explained variance of the full model, and repeated the multimodel inference approach. We report the mean summed Akaike weights per predictor and effect sizes across the 1000 models as the results for the selections.

To test for multicollinearity, Variance Inflation Factors (VIF) (Field, Miles, & Field, 2012) were derived using the function vif of the R-package “car” (Fox, Sanford, Fox, & Weisberg, 2011) applied to a standard linear model excluding the random effects and the interactions for each of the models. Collinearity was predictably high in the two chimpanzee communities between sex and rank (maximum VIF=5.4), as all males are higher-ranking than all females. Both were left in the model, as there was variation of rank values within each sex. Linear models with Gaussian error structure showed normal distribution of residuals. We tested for the presence of influential cases by systematically removing levels of the random effects (Field et al., 2012), which revealed that one young male had a disproportional impact on the effect of the sex combination of the grooming model in East community. We here report the results testing the impact of easily assessable parameters in East community excluding this individual for the grooming model, but have included the results of the full model in the supplementary material (Tab. S1). For Poisson models, we tested for overdispersion, which was not an issue (maximum dispersion parameter: 0.78).

*Relationship Types*

Interactions are easily predictable for an individual if relationships can be categorised into stereotypic “relationship types” (Bergman & Beehner, 2015) that structure how each dyad interacts. If all dyads belonging to one type in a community behave one way, and all other dyads behave in another, individuals do not have to make partner-specific decisions. Cluster analysis is an analytical tool that allows for the identification of relationships that follow similar rules across dyads in a community (Fischer et al., 2017).

For this analysis, each dyad in a group was represented once, by the non-directed, symmetric rates of grooming, body contact, proximity, food sharing, and aggression. These values were then entered into the cluster analysis. We used the social interaction rates rather than create a set of composite relationship indices (Fischer et al., 2017) to allow for the inclusion of interaction types that are not necessarily socio-positive or socio-negative. To statistically identify the number of distinct relationship types in each community, we used the “Optimal\_Clusters\_KMeans” function from the R package “ClusterR” (Mouselimis, 2018) to perform a cluster analysis. The algorithm identifies possible clusters of dyads, where dyads within each cluster are more similar to each other than dyads between clusters in the distribution of interactions. To assess the quality of each cluster solution, we used the average silhouette width as criterion for adequate cluster solutions (Kaufman & Rousseeuw, 1990). The silhouette value for a cluster solution is determined by the Euclidean distance of each point to every other point that is within the same or in a different cluster (Kaufman & Rousseeuw, 1990). The silhouette value can range from -1, if clusters completely overlap, to 1, indicating that the clusters are perfectly separated (Kaufman & Rousseeuw, 1990). Average silhouette widths above 0.5 are generally considered to represent clear cluster solutions (Kaufman & Rousseeuw, 1990); if no solution in our analyses exceeded 0.5, we examined the solution with the highest silhouette value to see if it approached that value. We then conducted k-means clustering (Tabachnick & Fidell, 2001) using the “KMeans\_rcpp” function from the “ClusterR” package to assign each dyad in the community to one of the clusters.

**RESULTS**

***Consistency***

Our measure of consistency, repeatedly selecting half of focal observation days and correlating the interaction rates with those of the other half, proved useful in identifying interaction types with insufficient information available (see Supplementary). In all three communities, contact aggressions and food sharing stood out as having the lowest number of interactions (around or below 1 average interaction per dyad). Both of them also stood out as for all communities, consistency values were below r=0.5 (Tab. 1). In our simulations, such low values only occurred when insufficient data was available to successfully approximate the underlying distributions of interactions, even in cases where the underlying distribution was highly consistent. For all other interaction types, consistency values were above r=0.5 in all communities. We excluded food sharing from subsequent analyses and combined contact aggressions with non-contact aggressions into an overall aggression category (Tab. 1). To be able to compare groups of different sizes, and interaction types with different occurrence rates, we tested how many interactions per dyad were necessary to reach a consistency value of r=0.5. Interaction types that reached this cut-off with fewer average interactions per dyad were considered more predictable than those that require more interactions per dyad to reach the cut-off.

Table 1: Overview of the datasets for each interaction type and group, and the results of the consistency measures. “Overall consistency” is the median of the repeated correlation between randomly selected halves for the full dataset available for an interaction type. “Standardised Consistency” and the standard deviation are the result of the repeated random selection of halves of subsets of different lengths, with the average number of interactions per dyad for which the median correlation coefficient exceeds r=0.5 as measure of how much information is needed to predict future interactions in a community.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Group** | **Interaction Type** | **IDs** | **Interactions** | **Overall Consistency** | **Standardised Consistency (Interactions/dyad)** | **SD** |
| Mangabey | Grooming | 23 | 1162 | 0.52 | 1.8 | 0.4 |
| Mangabey | Body Contact | 23 | 2218 | 0.51 | 7.4 | 1.4 |
| Mangabey | Proximity | 23 | 4373 | 0.51 | 14.5 | 2.5 |
| Mangabey | Aggression Non-contact | 23 | 971 | 0.58 | 1.3 | 0.3 |
| Mangabey | Aggression Contact | 23 | 210 | 0.24 | - | - |
| Mangabey | Aggression Total | 23 | 1181 | 0.64 | 1.3 | 0.2 |
| Mangabey | Supplant | 23 | 1219 | 0.69 | 2.1 | 0.5 |
| East | Grooming | 12 | 3099 | 0.75 | 4.7 | 2.0 |
| East | Body Contact | 12 | 1935 | 0.64 | 11.7 | 5.6 |
| East | Proximity | 12 | 2796 | 0.69 | 13.1 | 6.2 |
| East | Aggression Non-contact | 12 | 693 | 0.65 | 2.2 | 0.8 |
| East | Aggression Contact | 12 | 126 | 0.33 | - | - |
| East | Aggression Total | 12 | 819 | 0.67 | 2.6 | 0.9 |
| East | Food Sharing | 12 | 151 | 0.40 | - | - |
| East | Pant Grunt | 12 | 2429 | 0.92 | 0.9 | 0.1 |
| South | Grooming | 12 | 4693 | 0.81 | 4.2 | 2.5 |
| South | Body Contact | 12 | 1669 | 0.62 | 12.0 | 5.1 |
| South | Proximity | 12 | 2579 | 0.69 | 14.0 | 5.6 |
| South | Aggression Non-contact | 12 | 768 | 0.80 | 1.3 | 0.6 |
| South | Aggression Contact | 12 | 173 | 0.42 | - | - |
| South | Aggression Total | 12 | 941 | 0.79 | 1.3 | 0.6 |
| South | Food Sharing | 12 | 153 | 0.34 | - | - |
| South | Pant Grunt | 12 | 3350 | 0.93 | 1.4 | 0.00 |

*Mangabeys*

For the mangabeys, overall aggression rates (1.3 interactions/dyad, SD=0.2), grooming (1.8 interactions/dyad, SD=0.4), and supplants (2.1 interactions/dyad, SD=0.5), were among the most consistent behaviours we observed for all groups, indicating that individuals observing a subset of interactions in the community would be able to predict future interactions (Fig. 1, Tab. 1). Body contact (7.4 interactions/dyad, SD=1.4) and proximity (14.5 interactions/dyad, SD=2.5) were much less consistent.

*Chimpanzees*

As in the mangabeys, overall aggression rates were highly consistent in both chimpanzee communities (Table 1), more so in South (1.3 interactions/dyad, SD=0.6) than in East (2.6 interactions/dyad, SD=0.9). The larger standard deviation in the chimpanzees compared to the mangabeys might indicate changes of aggression patterns over time (see Supplementary). Pant grunt interactions in both communities showed the most predictable patterns (East: 0.9 interactions/dyad, SD=0.1; South: 1.4 interactions/dyad, SD=0.00). Grooming was less consistent than in the mangabeys (East: 4.7 interactions/dyad, SD=2.0; South: 4.2 interactions/dyad, SD=2.5), with the large standard deviation indicating changes in interaction patterns over the course of the study period. Body contact (East: 11.7 interactions/dyad, SD=5.6; South: 12.0 interactions/dyad, SD=5.1) and proximity (East: 13.1 interactions/dyad, SD=6.2; South: 14.0 interactions/dyad, SD=5.6) were considerably less predictable than the directed interaction types. This indicates that in all three communities, most dyads will feed and rest in close proximity with a wide variety of partners, while they direct interactions at a smaller and more stable subset of group members.



Figure 1: Spearman correlation between two halves of randomly selected subsets of the datasets for mangabeys (green), East chimpanzee community (gold) and South chimpanzee community (blue) for the different interaction types. The standardised consistency is marked by the average number of interactions per dyad where the median of correlation coefficients exceeds r=0.5. If that value is reached with fewer interactions per dyad, the distribution of interaction rates is more consistent. Distributions of correlation coefficients with a large spread indicate changes in interaction preference over time.

***Easily assessable parameters***

*Mangabeys*

In the mangabeys, body contact (R2 = 0.38) and proximity (R2 = 0.49) were explained moderately well by the fixed effects, with high dyadic association, low rank distance, and sex combination (female-female dyads having the lowest values) having equally strong impact on dyadic values in both interaction types, while kinship positively influenced body contact (Tab. 2). Aggression (R2 = 0.31) was influenced by the rank relationship between two individuals, with aggressions usually directed down the hierarchy, and by the sex of the receiver, with males receiving more aggressions. Supplants were expectedly well explained by the easily assessable parameters (R2 = 0.64), especially by dominance rank and sex, but also by dyadic association. Grooming was poorly explained by easily assessable parameters (R2 = 0.17), with kinship being the strongest indicator, while females were more likely to groom with each other, males did not groom with each other at all, and high-ranking individuals received more grooming. Thus, both sex and dominance rank influenced all interaction types, while kinship influenced who groomed and stayed in body contact, and association patterns only influenced spatial proximity and supplants.

*Chimpanzees*

In the East community, grooming (R2= 0.60; Tab. 2) was well explained by easily assessable parameters, particularly by association and a strong bias towards male-male grooming. Body contact (R2 = 0.46) and proximity (R2 = 0.52) were moderately well explained, most strongly by the dyadic association index, but also by male dyads being less likely than female and mixed dyads to stay in body contact. Pant grunts were well explained by the parameters (R2 = 0.65), predictably by dominance rank and sex, with males being the receiver of pant grunts more often than females. Aggression rates were poorly explained by the fixed effects of the model (R2 = 0.22), with high rank of the sender and low dyadic association being the strongest predictors, while low rank of the receiver and male sex of the sender also influenced interaction distributions. Dyadic association influenced all interaction types except pant grunts to a large degree, while dominance rank only influenced aggressions and pant grunt interactions. Sex played a moderate role for most interaction types, but strongly influenced grooming distribution.

In South, grooming was explained to a very high degree by basic attributes (R2 = 0.71), especially by the sex combination, being strongly biased towards male dyads. As in East community, body contact (R2 = 0.40) and proximity (R2 = 0.52) were explained moderately well by dyadic association and showed lower rates in male dyads. Pant grunts were predictably strongly influenced by the fixed effects of the model (R2 = 0.69), especially by dominance ranks, by the fact that kin pant grunted less than expected, and to a lesser degree receiver and sender sex. Aggression (R2 = 0.30) was less likely among kin and when the receiver was male and/or of high rank, and more likely when the sender was a male and/or high-ranking. Like in the mangabeys, kinship influenced grooming, and was associated with lower levels of aggression and pant grunts. Dyadic association patterns were less influential than in East community, but still influenced body contact and proximity. The impact of dominance rank did not differ from the other chimpanzee community and was less pronounced than in the mangabeys.

Table 2: Summary of the explained model variance (R2) containing the easily assessable parameters (sex combination, kinship, rank, and association), as well as the summed Akaike weights per predictor. Predicted values in italics, fixed effects that explained distributions better than expected are marked with \*.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Group | Interaction Type | R2 | Dyadic Association | Kin | Rank Interaction/ Difference | Rank Sender | Rank Receiver | Sex Interaction/ Combination | Sex Sender | Sex Receiver |
|  | ***Predicted*** |  | *0.38* | *0.38* | *0.08* | *0.43* | *0.43* | *0.08* | *0.43* | *0.43* |
| Mangabey | Grooming | ***0.17*** | 0.41 | 1\* | 0.19 | 0.70\* | 0.60\* | 0.39 | 0.73\* | 0.89\* |
| East | Grooming | ***0.60*** | 0.94\* | - | 0.05 | 0.38 | 0.48 | 0.96\* | 0.99\* | 0.97\* |
| South | Grooming | ***0.71*** | 0.33 | 0.44 | 0.07 | 0.46 | 0.33 | 1 | 1 | 1 |
| Mangabey | Aggression | ***0.31*** | 0.30 | 0.32 | 1\* | 1\* | 1\* | 0.17 | 0.37 | 0.97\* |
| East | Aggression | ***0.22*** | 0.95\* | - | 0.55\* | 0.98\* | 0.70\* | 0.12 | 0.86\* | 0.42 |
| South | Aggression | ***0.30*** | 0.41 | 1\* | 0.22 | 0.98\* | 0.78\* | 0.12 | 0.75\* | 0.57\* |
| Mangabey | Supplant | ***0.64*** | 1\* | 0.36 | 1\* | 1\* | 1\* | 0.97\* | 0.98\* | 0.98\* |
| East | Pant Grunt | ***0.65*** | 0.29 | - | 1 | 1 | 1 | - | 0.44 | 0.97\* |
| South | Pant Grunt | ***0.69*** | 0.23 | 1\* | 0.95\* | 1\* | 1\* | 0.14 | 0.89\* | 0.64\* |
|  | ***Predicted*** |  | *0.38* | *0.38* | *0.38* | *-* | *-* | *0.27* | *-* | *-* |
| Mangabey | Contact | ***0.39*** | 1\* | 0.65\* | 1\* | - | - | 0.97\* | - | - |
| East | Contact | ***0.46*** | 0.98\* | - | 0.24 | - | - | 0.60\* | - | - |
| South | Contact | ***0.40*** | 0.94\* | 0.26 | 0.19 | - | - | 0.99\* | - | - |
| Mangabey | Proximity | ***0.49*** | 1\* | 0.27 | 1\* | - | - | 1\* | - | - |
| East | Proximity | ***0.52*** | 1\* | - | 0.21 | - | - | 0.08 | - | - |
| South | Proximity | ***0.52*** | 0.99\* | 0.27 | 0.21 | - | - | 0.77\* | - | - |

***Relationship types***

We used cluster analysis on the interaction rates and association to identify distinct clusters of relationships. As a result of the consistency analysis, we removed food sharing and combined the two aggression variables. The interaction rates for each interaction type for the cluster solutions with the highest silhouette value, indicating the best differentiation between clusters, are depicted for each species in Tab. 3. Interaction rates for the excluded interaction types, contact aggressions and food sharing, were considerably lower than all other interaction types (less than 0.01 interactions per focal observation hour).

*Mangabeys*

For the mangabeys, no cluster solution using all interaction rates reached a silhouette value approaching 0.5 (maximum silhouette value: 0.3; see Supplementary Fig. S4); thus, there was likely no underlying cluster structure when taking all variables into account. The two spatial proximity measures might include noise due to the unstructured movement patterns of the species and not represent active partner choice, also indicated by the fact that association did not influence mangabey grooming or aggression patterns. We thus repeated the cluster analysis based only on grooming and aggression. Here, the best solution (silhouette value: 0.46; see Supplementary Fig. S5) included 4 clusters (Tab. 3; see Supplementary Fig. S6). The first one, which we would term “frequent affiliative” relationship type (10 female dyads, 1 mixed dyad) following Fischer et al., 2017, showed very high grooming rates (see Tab. 3 for average hourly rates) and medium aggression rates. The second cluster (“frequent agonistic” relationship type; 2 mixed dyads, 6 male dyads), was mainly defined by high aggression rates and absence of grooming. The third cluster (30 female, 32 mixed, 6 male dyads), showed low rates of grooming and medium rates of aggression, creating a “rare agonistic” relationship type. The fourth cluster showed low rates of both interaction types, comprising dyads who did not interact regularly in any way (“rare ambivalent” relationship type; 96 female, 67 mixed, 3 male dyads).

*Chimpanzees*

In the East community, the best cluster solution (silhouette value = 0.5; Fig. S7) identified four clusters (Tab. 3). The first two clusters, including two male dyads in the first and two female and a mixed dyad in the second cluster, could be labelled “frequent affiliative” relationships, as seen in the mangabeys. Both showed relatively low aggression rates (see Tab. 3, Fig. S8). While the male dyads had very high grooming values, the female and mixed dyads had high rates of body contact and proximity values, and high levels of grooming for these sex combinations. The third cluster represented a “frequent ambivalent” relationship type, comprising 6 male dyads and showing high levels of grooming and high levels of aggression. The fourth cluster, comprising 2 male, 34 mixed, and 19 female dyads, showed few interactions of any kind and the lowest association values, equivalent to the “rare ambivalent” relationship type in mangabeys.

In South community, the best cluster solution (silhouette value = 0.48, Fig. S8) identified three clusters (Tab. 3): The first relationship type, with 4 female and 1 mixed dyads (mother-son), included dyads with high body contact and proximity values, average grooming rates, but low aggression rates, equivalent to the female “frequent affiliative” cluster in East (see Fig. S9). The second relationship type, including 8 male dyads, included frequent ambivalent relationships with high interaction frequencies of both aggression and grooming, but low body contact rates. The third cluster (2 male dyads, 34 mixed dyads, 17 female dyads) had lower grooming and proximity rates than the other two, and on average very few aggressions, equivalent to the ”rare ambivalent” cluster in the other two groups.

Table 3: Results of the cluster analysis for the three communities. Values depict the mean interaction rates per hour of each interaction type for each cluster. For the mangabeys, after removing spatial variables, 4 clusters were found (silhouette value: 0.46). The best cluster solution for East had 4 clusters (silhouette value: 0.50); the best cluster solution for South had 3 clusters (silhouette value: 0.48). Grooming and chimpanzee body contact and proximity in min/h, while aggressions represent events/hour.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Group** | **Cluster** | **N dyads** | **Grooming** | **Body Contact** | **Proximity** | **Aggression** |
| **Mangabey** | **Frequent Affiliative** | 11 | 0.50 | - | - | 0.03 |
| **Frequent Agonistic** | 8 | 0.00 | - | - | 0.11 |
| **Rare Agonistic** | 68 | 0.06 | - | - | 0.04 |
| **Rare Ambivalent** | 166 | 0.05 | - | - | 0.01 |
| **East** | **Frequent Affiliative Male** | 2 | 1.08 | 0.29 | 0.77 | 0.01 |
| **Frequent Affiliative Female** | 3 | 0.33 | 1.04 | 1.68 | 0.01 |
| **Frequent Ambivalent** | 6 | 0.33 | 0.26 | 0.56 | 0.03 |
| **Rare Ambivalent** | 55 | 0.08 | 0.17 | 0.24 | 0.01 |
| **South** | **Frequent Affiliative** | 5 | 0.31 | 0.60 | 1.02 | 0.00 |
| **Frequent Ambivalent** | 8 | 1.10 | 0.07 | 0.39 | 0.04 |
| **Rare Ambivalent** | 53 | 0.17 | 0.11 | 0.21 | 0.01 |

**DISCUSSION**

Establishing measures of predictability of social interactions and the resulting relationships between individuals is necessary to understand the complexity of a social group from the perspective of the individual (Dunbar & Shultz, 2010; Lukas & Clutton-Brock, 2018). Here, we applied three methods of data analysis to identify different sources of predictability in the social relationships of chimpanzees and sooty mangabeys. Our premise was that interactions are more predictable for participants and bystanders if interaction distributions are consistent over time, based on parameters that are easily assessable for group members (sex, rank, kinship, association), or structured by the existence of distinct relationship types (Bergman & Beehner, 2015). Our results showed that across communities and species, interaction types vary in predictability, indicating that multi-dimensional measures of relational complexity might be able to pinpoint sources of unpredictability of social relationships that remain unaccounted for in one-dimensional structural measures.

This study introduces a consistency measure, repeatedly dividing the dataset into halves and comparing how well these predict each other, which serves two functions. Researchers can use it to find out whether they have collected sufficient data for their dataset to be internally consistent, given a community of a certain size and an interaction type with a specific diversity of partner choice (Sánchez-Tójar et al., 2017). In our sample, despite pooling 18 months of data, food sharing and contact aggressions was observed at such low rates in all three communities that observing the group at a certain time point would make it impossible to predict their behaviour at another time point. We generally assume that randomly selected focal follows allow us to also make statements about interaction rates on those days on which we do not observe an individual (Davis et al., 2018), but this might not be the case for rare interaction types. One way to understand patterns driving interaction patterns for rare interaction types would be to test the factors influencing decisions by comparing each partner choice an individual makes against the alternatives they did not choose (Mielke et al., 2018; Samuni et al., 2018). In order to assess changes in relationships over time, there has been a trend to cut datasets into smaller subsets and then compare network overlap between these, assuming that the data in each is sufficient to depict the underlying distribution in the community. With our consistency measure, seasonality and change could be established if smaller subsets would show higher consistency than larger subsets, as random subsets retained consistent time intervals. This was not the case for any interaction type, even though some interaction types showed high standard variation, and indication that consistency is high during some times but not others.

The standardized consistency measure allowed us to segregate interaction types into those that needed either high or low amounts of information to predict future interactions. We included feeding supplants and pant grunts as proof of concept, and both of them were highly consistent in the two species, indicating generally stable hierarchies (Sánchez-Tójar et al., 2017). Despite being the larger community, mangabey interactions were generally more predictable than chimpanzee interaction patterns, with fewer grooming and body contact interactions per dyad needed to reach the consistency cut-off in mangabeys. Directed interactions (grooming, aggression, pant grunts/supplants) were consistent despite the inclusion of 18 months of data per community, indicating that most dyads interacted at relatively constant rates throughout the study period. The higher consistency of mangabey interactions could be the result of a highly stable dominance hierarchy (Mielke et al., 2017), few demographic changes (Borgeaud, Sosa, Sueur, & Bshary, 2017), and a relatively low diversity of partner choice for most individuals (Duboscq et al., 2017; Silk, Cheney, & Seyfarth, 2013), while both chimpanzee communities displayed rank changes throughout and all group members interacted with each other. Spatial proximity was much less predictable than directed interactions, most likely because a certain level of tolerance in foraging and resting extends to most group members, adding random noise that is not present in directed interactions (Castles et al., 2014). Alternatively, factors influencing proximity might be more variable than can be captured in aggregated measures. An individual that has to accurately predict future spatial proximity between individuals would therefore have to observe more interactions than individuals predicting aggressive interactions. Just like rare interaction types, common but highly inconsistent interaction types could add noise to social relationship indices or when comparing network overlap.

In contrast to the differences in consistency, the explained variance of easily assessable parameters was remarkably similar across species. This result does not support predictions based on the differences in hierarchy steepness (Balasubramaniam et al., 2012), tolerance (Duboscq et al., 2017), kinship structure (Langergraber et al., 2007; Range, 2006), and fission-fusion dynamics (Amici, Aureli, & Call, 2008) between sooty mangabeys and chimpanzees. While the factors explaining interaction distributions generally followed the predictions made based on previous research, the effect sizes were largely comparable between species, with the possible exception of grooming. Grooming rates were very high for almost all male dyads in both chimpanzee communities, making sex a strong predictor for grooming distributions in this species (Gomes et al., 2009). However, this does not necessarily indicate which partner within the sex class individuals choose. In mangabeys, while kinship, sex, and rank influenced grooming distributions, the variance they explained was low. The reason for this was that many dyads in each sex, rank, and kin combination groomed at very low rates or not at all, so the fact that a dyad did not groom at all does not allow the model to tell whether the dyad is male, mixed, or female. It is possible that we underestimate the impact of kinship on grooming in mangabeys because we only know mother-offspring dyads and not maternal or paternal siblings; however, some known kin dyads did not have high grooming rates and studies in captivity for this species also reported an absence of strong kin bias (Ehardt, 1988). In the South chimpanzee community, where kin were available as partners, individuals directed fewer aggressions and pant grunts at their relatives, indicating reduced conflict in those dyads.

The overall explained variance of fixed effects for aggression, pant grunts/supplants, body contact, and proximity did not differ markedly between the two species. Predictability based on the parameters was, as expected, highest for pant grunts/supplants (due to the circularity of including rank as a predictor), while they could explain about half of the variance between dyads for the spatial proximity measures. Aggression, though consistent, was not well explained by the combination of easily assessable parameters, probably because aggression patterns will often be determined by access to resources in specific situations (Heesen, Rogahn, Macdonald, Ostner, & Schülke, 2014). The two chimpanzee communities showed remarkably similar patterns, with the only difference being a stronger impact of dyadic association on grooming and aggression in the East community. In contrast to recent papers postulating cultural differences in the spatial proximity and grooming patterns of neighbouring chimpanzee communities (van Leeuwen, Cronin, & Haun, 2018), our study with large datasets for two wild communities did not find any clear-cut differences that might indicate cultural processes in those interaction types, or aggression. This replicates previous results showing no differences in the rates for these interaction types in the two communities, while differences in party sizes and group-level cooperation exist (Preis, Samuni, Deschner, Crockford, & Wittig, in press). In both species, interactions were structured along kinship, rank, and sex, making a good portion of them predictable using very basic rules. Other, more transient parameters, such as resource possession or reproductive state, and the simple long-term preference for certain partners, will probably allow individuals to predict interactions in the short-term more accurately. These transient parameters indicate more differentiated and complex rules underlying decision-making, pointing at an increase in relational complexity that will influence both species.

We applied cluster analysis to the interaction profiles of each dyad to identify distinct relationship types (Bergman & Beehner, 2015; Fischer et al., 2017). For the mangabeys, spatial proximity stood in no relation to grooming and aggressions, and no cluster solution was found using all interaction types, again indicating that spatial proximity in this species is not an expression of an underlying tendency to interact prosocially (Castles et al., 2014). Using only grooming and aggressions, we found four relationship types that overlapped closely with those described by Fischer et al. (2017) for Barbary macaques, despite body contact playing a different role in that species. A small subset of dyads had high-frequency grooming interactions and few aggressions, indicative of strong social bonds (Silk et al., 2010). Some dyads, mainly adult males, showed elevated aggression rates but no grooming. The majority of dyads in the community had low interaction rates, some with more aggressive and some with more grooming interactions. Social relationships are therefore almost distributed along a continuum from “negative” to “positive” that might make it easy for individuals to categorize relationship strength in other dyads (Borgeaud, Schnider, Krützen, & Bshary, 2017). In contrast, high levels of spatial proximity set apart a number of female and mixed dyads in chimpanzees, making body contact and proximity potentially useful in assigning social bonds in dyads that are unlikely to groom a lot (Lehmann & Boesch, 2009). The majority of male dyads in the chimpanzees (14 out of 20 dyads) showed high rates of both grooming and aggression, creating a “frequent ambivalent” cluster that does not exist in the mangabeys and Barbary macaques (Fischer et al., 2017). The high consistency of the aggression distribution indicates that this is not simply the result from individuals switching whom they aggress when there are rank changes, but that individuals show high levels of aggression and affiliation at the same time. Thus, there is considerable overlap in the relationship types of the two species, especially among females. Predictability might be lower and relational complexity higher in chimpanzee males, where positive and negative interactions co-exist in dyads and individuals will need additional information to determine whether an approaching group member will cooperate with them or harm them. It would be important to ascertain whether this pattern holds if more than two directed interaction types are included, e.g., if the availability of suitable food sharing data would lead to the creation of additional clusters or just follow the pattern established by grooming.

Combining the three relational complexity measures allowed us to paint a more comprehensive picture of the challenges facing sooty mangabeys and Western chimpanzees in navigating their social relationships than would have been possible by focusing on one-dimensional measures of social complexity such as group size. As predicted, matrilineal sooty mangabeys showed higher levels of consistency in how their interactions where distributed than chimpanzees, meaning individuals have to probably observe fewer interactions between dyads to predict future interaction patterns. This was the case despite the fact that the mangabey community included the largest number of adult individuals. The difference in predictability was also reflected in the presence of clearly affiliative and agonistic relationship types in mangabeys, matched by the affiliative relationships of some female chimpanzee dyads, while the ambivalent relationships of male chimpanzees created higher levels of uncertainty as to the outcome of dyadic encounters. Importantly, these differences in consistency and relationship types were not explained by differences in how predictable interaction patterns were based on kinship, dominance rank, sex, or association. While species differences existed in the factors underlying interaction distributions, the overall explained variance was largely similar, with the possible exception of grooming. The difference in fission-fusion dynamics could be responsible for less consistent interaction patterns in the chimpanzees, as individuals have to show behavioural flexibility when they are constrained in their access to preferred partners, and interact with individuals based on availability (Amici et al., 2008), a limitation mangabeys do not face. At the same time, spatial proximity showed high levels of noise in the cohesive movement system of the mangabeys, indicating that while there was assortative mixing due to rank, sex, as well as kin (Carter, Seddon, Frère, Carter, & Goldizen, 2013), the resulting patterns did not necessarily correlate with grooming or aggression.

The three metrics presented here create a toolkit that can be applied to additional species and interaction types and allows for a standardised representation of the relational complexity of a species, based on how predictable interactions are. Usually, researchers present one of these metrics for one interaction type of their study species in a publication, often using different methods. Because available information is distributed, focused on particular interaction types, or differs between studies, it is necessary to revert to simple representations of complexity (e.g., group size, hierarchy steepness) when comparing study species. One disadvantage is the direct comparison between interaction types that are shared between species, not accounting for differences in sheer interaction repertoire size. Also, only dyadic interactions are included, while triadic (such as third-party interventions) and group-level interactions (such as territorial defence, predator deterrence, or hunting) might increase unpredictability considerably. Standardised approaches, such as the one presented here, facilitate concise communication about how relationships are structured in a primate system and optimises information exchange in scientific publications. For example, while we mainly focus on the explained variance, the impact of different easily assessable parameters presented here yields itself directly to replication and comparison of important features across study species. We show that a standardised approach to assess social complexity is necessary to refine and clarify hypotheses about its effect on cognitive abilities within, between and among species.

**References**

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3), 227–266. https://doi.org/10.1080/14794802.2011.585831

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, *18*(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Anderson, C., & McShea, D. W. (2001). Individual versus social complexity, with particular reference to ant colonies. *Biological Reviews*, *76*(2), 211–237. https://doi.org/10.1017/S1464793101005656

Arnold, K., & Whiten, A. (2003). Grooming interactions among the chimpanzees of the Budongo Forest, Uganda: Tests of five explanatory models. *Behaviour*, *140*(4), 519–552. https://doi.org/10.1163/156853903322127968

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., … Van Schaik, C. P. (2008). Fission‐fusion dynamics. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., … De Waal, F. B. M. (2012). Hierarchical Steepness, Counter-Aggression, and Macaque Social Style Scale. *American Journal of Primatology*, *74*(10), 915–925. https://doi.org/10.1002/ajp.22044

Barrett, L., Gaynor, D., & Henzi, S. P. P. (2002). A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Animal Behaviour*, *63*(6), 1047–1053. https://doi.org/10.1006/anbe.2002.3008

Barrett, L., Henzi, P., & Rendall, D. (2007). Social brains, simple minds: does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 561–575. https://doi.org/10.1098/rstb.2006.1995

Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1599), 2108–2118. https://doi.org/10.1098/rstb.2012.0113

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1420), 665. https://doi.org/10.1098/rspb.1999.0687

Barton, K. (2018). R Package ’MuMIn.

Bergman, T. J., & Beehner, J. C. (2015). Measuring social complexity. *Animal Behaviour*, *103*, 203–209. https://doi.org/10.1016/j.anbehav.2015.02.018

Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical Classification by Rank and Kinship in Baboons. *Science*, *302*(5648).

Boesch, C., & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford: Oxford University Press.

Borgeaud, C., Schnider, A., Krützen, M., & Bshary, R. (2017). Female vervet monkeys fine-tune decisions on tolerance versus conflict in a communication network. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1867), 20171922. https://doi.org/10.1098/rspb.2017.1922

Borgeaud, C., Sosa, S., Sueur, C., & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. *Animal Behaviour*, *134*, 155–165. https://doi.org/10.1016/j.anbehav.2017.09.028

Borgeaud, C., van de Waal, E., & Bshary, R. (2013). Third-party ranks knowledge in wild vervet monkeys (Chlorocebus aethiops pygerythrus). *PLoS ONE*, *8*(3), 8–11. https://doi.org/10.1371/journal.pone.0058562

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical Information-Theoretic-approach*. Springer. https://doi.org/10.1016/j.ecolmodel.2003.11.004

Byrne, R. W., & Whiten, A. (1989). *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford: Oxford University Press.

Carter, K. D., Seddon, J. M., Frère, C. H., Carter, J. K., & Goldizen, A. W. (2013). Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. *Animal Behaviour*, *85*(2), 385–394. https://doi.org/10.1016/j.anbehav.2012.11.011

Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlishaw, G., & Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Animal Behaviour*. Academic Press. https://doi.org/10.1016/j.anbehav.2014.07.023

Chan, S., Fushing, H., Beisner, B. A., & McCowan, B. (2013). Joint modeling of multiple social networks to elucidate primate social dynamics: I. Maximum entropy principle and network-based interactions. *PLoS ONE*, *8*(2), e51903. https://doi.org/10.1371/journal.pone.0051903

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*. Hillsdale, NJ: Erlbaum.

Connor, R. C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*(1480), 587–602. https://doi.org/10.1098/rstb.2006.1997

Davis, G. H., Crofoot, M. C., & Farine, D. R. (2018). Estimating the robustness and uncertainty of animal social networks using different observational methods. *Animal Behaviour*, *141*, 29–44. https://doi.org/10.1016/j.anbehav.2018.04.012

Dobson, A. J. (2002). *An introduction to generalized linear models*. London: Chapman & Hall/CRC.

Douglas, P. H., Ngonga Ngomo, A. C., & Hohmann, G. (2017). A novel approach for dominance assessment in gregarious species: ADAGIO. *Animal Behaviour*. Academic Press. https://doi.org/10.1016/j.anbehav.2016.10.014

Duboscq, J., Neumann, C., Agil, M., Perwitasari-Farajallah, D., Thierry, B., & Engelhardt, A. (2017). Degrees of freedom in social bonds of crested macaque females. *Animal Behaviour*, *123*, 411–426. https://doi.org/10.1016/j.anbehav.2016.11.010

Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, *16*(4), 681–694. https://doi.org/10.1017/S0140525X00032325

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*(5843), 1344–7. https://doi.org/10.1126/science.1145463

Dunbar, R. I. M., & Shultz, S. (2010). Bondedness and sociality. *Behaviour*. https://doi.org/10.1163/000579510X501151

Ehardt, C. L. (1988). Absence of strongly kin-preferential behavior by adult female sooty mangabeys (*Cercocebus atys*). *American Journal of Physical Anthropology*, *76*(2), 233–43. https://doi.org/10.1002/ajpa.1330760212

Farine, D. R., & Strandburg-Peshkin, A. (2015). Estimating uncertainty and reliability of social network data using Bayesian inference. *Royal Society Open Science*, *2*(9), 150367. https://doi.org/10.1098/rsos.150367

Fedurek, P., & Lehmann, J. (2017). The effect of excluding juveniles on apparent adult olive baboons (Papio anubis) social networks. *PLoS ONE*, *12*(3), e0173146. https://doi.org/10.1371/journal.pone.0173146

Field, A. P., Miles, J., & Field, Z. (2012). *Discovering Statistics Using R*. New York: Sage. https://doi.org/10.1111/insr.12011\_21

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour*, *130*, 57–66. https://doi.org/10.1016/j.anbehav.2017.06.003

Flack, J. C. (2012). Multiple time-scales and the developmental dynamics of social systems. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1597), 1802–10. https://doi.org/10.1098/rstb.2011.0214

Foerster, S., Franz, M., Murray, C. M., Gilby, I. C., Feldblum, J. T., Walker, K. K., & Pusey, A. E. (2016). Chimpanzee females queue but males compete for social status. *Scientific Reports*, *6*(1), 1–11. https://doi.org/10.1038/srep35404

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 Behaviour*, *105*, 139–152. https://doi.org/10.1016/j.anbehav.2015.04.012

Fox, L., Sanford, W., Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression* (Second). Thousand Oaks, CA: Sage.

Gero, S., Bejder, L., Whitehead, H., Mann, J., & Connor, R. C. (2005). Behaviourally specific preferred associations in bottlenose dolphins, Tursiops spp. *Canadian Journal of Zoology*, *83*(12), 1566–1573. https://doi.org/10.1139/z05-155

Goffe, A. S., Zinner, D., & Fischer, J. (2016). Sex and friendship in a multilevel society: behavioural patterns and associations between female and male Guinea baboons. *Behavioral Ecology and Sociobiology*, *70*(3), 323–336. https://doi.org/10.1007/s00265-015-2050-6

Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1657), 699–706. https://doi.org/10.1098/rspb.2008.1324

Guillermo Paz-Y-Miño, C., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, *430*(7001), 778–781. https://doi.org/10.1038/nature02723

Gumert, M. D. (2007). Payment for sex in a macaque mating market. *Animal Behaviour*, *74*(6), 1655–1667. https://doi.org/10.1016/j.anbehav.2007.03.009

Halford, G. S., Wilson, W. H., & Phillips, S. (1998). Processing capacity defined by relational complexity: Implications for comparative, developmental, and cognitive psychology. *Behavioral and Brain Sciences*, *21*(6), 803–864. https://doi.org/10.1017/S0140525X98001769

Heesen, M., Rogahn, S., Macdonald, S., Ostner, J., & Schülke, O. (2014). Predictors of food-related aggression in wild Assamese macaques and the role of conflict avoidance. *Behavioral Ecology and Sociobiology*, *68*(11), 1829–1841. https://doi.org/10.1007/s00265-014-1792-x

Hemelrijk, C. K. (1999). An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1417), 361. https://doi.org/10.1098/rspb.1999.0646

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man, New Series*, *11*(1), 1–17. https://doi.org/10.2307/2800384

Hirsch, B. T., Prange, S., Hauver, S. A., & Gehrt, S. D. (2013). Genetic relatedness does not predict racoon social network structure. *Animal Behaviour*, *85*(2), 463–470. https://doi.org/10.1016/j.anbehav.2012.12.011

Hirsch, B. T., Stanton, M. A., & Maldonado, J. E. (2012). Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. *PLoS ONE*, *7*(5), e37301. https://doi.org/10.1371/journal.pone.0037301

Humphrey, N. K. The social function of intellect. (P. P. G. Bateson & R. A. Hinde, Eds.), 37 Growing Points in Ethology § (1976). Cambridge: Cambridge University Press. https://doi.org/10.2307/375925

Kaburu, S. S. K., & Newton-Fisher, N. E. (2015). Egalitarian despots: Hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, Pan troglodytes. *Animal Behaviour*, *99*, 61–71. https://doi.org/10.1016/j.anbehav.2014.10.018

Kaburu, S. S. K., & Newton-Fisher, N. E. (2016). Bystanders, parcelling, and an absence of trust in the grooming interactions of wild male chimpanzees. *Scientific Reports*, (October 2015), 1–10. https://doi.org/10.1038/srep20634

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

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*(4), 343–356. https://doi.org/10.1007/s10329-009-0153-2

Kaufman, L., & Rousseeuw, P. J. (1990). *Finding Groups in Data*. Hoboken, NJ, USA: John Wiley & Sons, Inc.

Koski, S. E., de Vries, H., van de Kraats, A., & Sterck, E. H. M. (2012). Stability and change of social relationship quality in captive chimpanzees (Pan troglodytes). *International Journal of Primatology*, *33*(4), 905–921. https://doi.org/10.1007/s10764-012-9623-2

Kulik, L., Muniz, L., Mundry, R., & Widdig, A. (2012). Patterns of interventions and the effect of coalitions and sociality on male fitness. *Molecular Ecology*, *21*(3), 699–714. https://doi.org/10.1111/j.1365-294X.2011.05250.x

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*, *104*(19), 7786–7790. https://doi.org/10.1073/pnas.0611449104

Langergraber, K. E., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (Pan troglodytes). *American Journal of Primatology*, *71*, 840–851. https://doi.org/10.1002/ajp.20711

Lea, A. J., Blumstein, D. T., Wey, T. W., & Martin, J. G. A. (2010). Heritable victimization and the benefits of agonistic relationships. *Proceedings of the National Academy of Sciences*, *107*(50), 21587–21592. https://doi.org/10.1073/pnas.1009882107

Lehmann, J., Andrews, K., & Dunbar, R. (2010). Social networks and social complexity in female-bonded primates. In R. I. M. Dunbar, C. Gamble, & J. Gowlett (Eds.), *Social Brain, Distributed Mind*. Oxford: Oxford University Press.

Lehmann, J., & Boesch, C. (2008). Sexual differences in chimpanzee sociality. *International Journal of Primatology*, *29*(1), 65–81. https://doi.org/10.1007/s10764-007-9230-9

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, Pan troglodytes. *Animal Behaviour*, *77*(2), 377–387. https://doi.org/10.1016/j.anbehav.2008.09.038

Leinfelder, I., De Vries, H., Deleu, R., & Nelissen, M. (2001). Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *American Journal of Primatology*, *55*(1), 25–42. https://doi.org/10.1002/ajp.1036

Lukas, D., & Clutton-Brock, T. (2018). Social complexity and kinship in animal societies. *Ecology Letters*, *0049*, 1–24. https://doi.org/10.5063/F1FB513K

Lusseau, D., Whitehead, H., & Gero, S. (2008). Incorporating uncertainty into the study of animal social networks. *Animal Behaviour*, *75*(5), 1809–1815. https://doi.org/10.1016/j.anbehav.2007.10.029

Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2009). The social network structure of a wild meerkat population: 2. Intragroup interactions. *Behavioral Ecology and Sociobiology*, *64*(1), 81–95. https://doi.org/10.1007/s00265-009-0820-8

Madden, J. R., Nielsen, J. F., & Clutton-Brock, T. H. (2012). Do networks of social interactions reflect patterns of kinship? *Current Zoology*, *58*(2), 319–328. https://doi.org/10.1093/czoolo/58.2.319

McShea, D. W. (1996). Metazoan complexity and evolution: Is there a trend? *Evolution*. https://doi.org/10.1111/j.1558-5646.1996.tb03861.x

Mielke, A., Crockford, C., & Wittig, R. M. (n.d.). Rank changes in female chimpanzees in Tai National Park. In C. Boesch & R. M. Wittig (Eds.), *The Tai Chimpanzees: 40 Years of Research*. Cambridge: Cambridge University Press.

Mielke, A., Preis, A., Samuni, L., Gogarten, J. F., Wittig, R. M., & Crockford, C. (2018). Flexible decision-making in grooming partner choice in sooty mangabeys and chimpanzees. *Royal Society Open Science*, *5*(172143).

Mielke, A., Samuni, L., Preis, A., Gogarten, J. F., Crockford, C., & Wittig, R. M. (2017). Bystanders intervene to impede grooming in Western chimpanzees and sooty mangabeys. *Royal Society Open Science*, *4*(11), 171296. https://doi.org/10.1098/rsos.171296

Miller, J. A., Pusey, A. E., Gilby, I. C., Schroepfer-Walker, K., Markham, A. C., & Murray, C. M. (2014). Competing for space: Female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, *87*(C), 147–152. https://doi.org/10.1016/j.anbehav.2013.10.023

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Moscovice, L. R., Douglas, P. H., Martinez-Iñigo, L., Surbeck, M., Vigilant, L., & Hohmann, G. (2017). Stable and fluctuating social preferences and implications for cooperation among female bonobos at LuiKotale, Salonga National Park, DRC. *American Journal of Physical Anthropology*, *163*(1), 158–172. https://doi.org/10.1002/ajpa.23197

Mouselimis, L. (2018). R Package ClusterR.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Naud, A., Chailleux, E., Kestens, Y., Bret, C., Desjardins, D., Petit, O., … Sueur, C. (2016). Relations between spatial distribution, social affiliations and dominance hierarchy in a semi-free Mandrill population. *Frontiers in Psychology*, *7*(MAY), 612. https://doi.org/10.3389/fpsyg.2016.00612

Oliveira, R. F., McGregor, P. K., & Latruffe, C. (1998). Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1401), 1045–1049. https://doi.org/10.1098/rspb.1998.0397

Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of “friendships” to female baboons: experimental and observational evidence. *Anim. Behav*, *54*, 599–614. https://doi.org/10.1006/anbe.1996.0457

Pearson, H. C. (2009). Influences on dusky dolphin (Lagenorhynchus obscurus) fission-fusion dynamics in Admiralty Bay, New Zealand. *Behavioral Ecology and Sociobiology*, *63*(10), 1437–1446. https://doi.org/10.1007/s00265-009-0821-7

Preis, A., Samuni, L., Deschner, T., Crockford, C., & Wittig, R. M. (n.d.). Group specific social dynamics affect urinary ocytocin levels in Tai male chimpanzees. In C. Boesch & R. M. Wittig (Eds.), *The Tai Chimpanzees: 40 Years of Research*. Cambridge: Cambridge University Press.

Preis, A., Samuni, L., Deschner, T., Crockford, C., & Wittig, R. M. (2019). Urinary cortisol, aggression, dominance and competition in wild, West African male chimpanzees. *Frontiers in Ecology and Evolution*.

Preis, A., Samuni, L., Mielke, A., Deschner, T., Crockford, C., & Wittig, R. M. (2018). Urinary oxytocin levels in relation to post-conflict affiliations in wild male chimpanzees (Pan troglodytes verus). *Hormones and Behavior*, *105*, 28–40. https://doi.org/10.1016/j.yhbeh.2018.07.009

Puga-Gonzalez, I., Hildenbrandt, H., & Hemelrijk, C. K. (2009). Emergent patterns of social affiliation in primates, a model. *PLoS Computational Biology*, *5*(12), e1000630. https://doi.org/10.1371/journal.pcbi.1000630

Ramos-Fernández, G., Boyer, D., & Gómez, V. P. (2006). A complex social structure with fission-fusion properties can emerge from a simple foraging model. *Behavioral Ecology and Sociobiology*, *60*(4), 536–549. https://doi.org/10.1007/s00265-006-0197-x

Ramos-Fernandez, G., King, A. J., Beehner, J. C., Bergman, T. J., Crofoot, M. C., Di Fiore, A., … Boyer, D. (2018). Quantifying uncertainty due to fission–fusion dynamics as a component of social complexity. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1879), 20180532. https://doi.org/10.1098/rspb.2018.0532

Range, F. (2006). Social behavior of free-ranging juvenile sooty mangabeys (Cercocebus torquatus atys). *Behavioral Ecology and Sociobiology*, *59*(4), 511–520. https://doi.org/10.1007/s00265-005-0076-x

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*, *56*(3), 137–153. https://doi.org/10.1002/ajp.1070

Sambrook, T., & Whiten, A. (1997). On the nature of complexity in cognitive and behavioural science. *Theory & Psychology*, *7*(2), 191–213. https://doi.org/10.1177/0959354397072004

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B*, *285*(1888), 20181643. https://doi.org/10.1098/rspb.2018.1643

Sánchez-Tójar, A., Schroeder, J., & Farine, D. R. (2017, November 27). A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. (J. Morand-Ferron, Ed.), *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.12776

Schielzeth, H. (2010). Simple means to improve the interpretability ofregression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. https://doi.org/10.1093/beheco/arn145

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, *62*, 265–271. https://doi.org/10.1006/anbe.2001.1750

Schino, G., & Aureli, F. (2017). Reciprocity in group-living animals: Partner control versus partner choice. *Biological Reviews*, *92*(2), 665–672. https://doi.org/10.1111/brv.12248

Shizuka, D., & Farine, D. R. (2016). Measuring the robustness of network community structure using assortativity. *Animal Behaviour*, *112*, 237–246. https://doi.org/10.1016/j.anbehav.2015.12.007

Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (Papio cynocephalus) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, *61*(2), 197–204. https://doi.org/10.1007/s00265-006-0250-9

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., … Cheney, D. L. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, *64*(11), 1733–1747. https://doi.org/10.1007/s00265-010-0986-0

Silk, J. B., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology*, *22*(5), 213–225. https://doi.org/10.1002/evan.21367

Smith, J. E., Memenis, S. K., & Holekamp, K. E. (2007). Rank-related partner choice in the fission-fusion society of the spotted hyena (Crocuta crocuta). *Behavioral Ecology and Sociobiology*, *61*(5), 753–765. https://doi.org/10.1007/s00265-006-0305-y

Tabachnick, B. G., & Fidell, L. S. (2001). *Using multivariate statistics* (4th Editio). Boston: Allyn and Bacon.

Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (1999). The Infuence of Phylogeny on the Social Behaviour of Macaques, 602–617.

Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2014). Kinship and dominance rank influence the strength of social bonds in female geladas (Theropithecus gelada). *International Journal of Primatology*, *35*(1), 288–304. https://doi.org/10.1007/s10764-013-9733-5

van Leeuwen, E. J. C., Cronin, K. A., & Haun, D. B. M. (2018). Population-specific social dynamics in chimpanzees. *Proceedings of the National Academy of Sciences*, *115*(45), 11393–11400. https://doi.org/10.1073/pnas.1722614115

Wessling, E. G., Kühl, H. S., Mundry, R., Deschner, T., & Pruetz, J. D. (2018). The costs of living at the edge: Seasonal stress in wild savanna-dwelling chimpanzees. *Journal of Human Evolution*, *121*, 1–11. https://doi.org/10.1016/j.jhevol.2018.03.001

Wey, T. W., & Blumstein, D. T. (2010). Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, *79*(6), 1343–1352. https://doi.org/10.1016/j.anbehav.2010.03.008

Whitehead, H. (2008a). *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago, USA: University of Chicago Press. https://doi.org/10.1017/CBO9781107415324.004

Whitehead, H. (2008b). Precision and power in the analysis of social structure using associations. *Animal Behaviour*, *75*(3), 1093–1099. https://doi.org/10.1016/j.anbehav.2007.08.022

Whiten, A. (2000). Social complexity and social intelligence. In *The nature of intelligence* (Vol. 233, pp. 185-96; discussion 196-201). Chichester, UK: Wiley.

Wittig, R. M., & Boesch, C. (2003). “Decision-making” in conflicts of wild chimpanzees (Pan troglodytes): An extension of the Relational Model. *Behavioral Ecology and Sociobiology*, *54*(5), 491–504. https://doi.org/10.1007/s00265-003-0654-8

Wittig, R. M., Crockford, C., Langergraber, K. E., & Zuberbühler, K. (2014). Triadic social interactions operate across time: a field experiment with wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20133155. https://doi.org/10.1098/rspb.2013.3155

Wittiger, L., & Boesch, C. (2013). Female gregariousness in Western Chimpanzees (Pan troglodytes verus) is influenced by resource aggregation and the number of females in estrus. *Behavioral Ecology and Sociobiology*, *67*(7), 1097–1111. https://doi.org/10.1007/s00265-013-1534-5