



Patterns of female social relationships in a primate with female-biased dispersal

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In socially living mammals, females often form highly differentiated and stable social relationships, commonly with genetically related individuals, which leads to social clusters within groups (i.e. matriline). However, in primates, research on female social relationships commonly focuses on species and populations with female philopatry and the frequent occurrence of affiliative and agonistic behaviours. Therefore, our aim was to investigate the long-term patterns of female social relationships in a primate with female-biased dispersal, where affiliative and agonistic behaviours among females are rare. We analysed 9 years of continuous data from female Ugandan red colobus monkeys, *Ptilocolobus tephrosceles*, in Kibale National Park, Uganda, and used spatial proximity to establish social networks for 3- and 6-month periods. Then, we investigated the differentiation, stability and clustering of social relationships for each of these periods using several approaches. As expected for a primate with female-biased dispersal, our results largely confirmed the absence of temporally stable social relationships and social clusters within the group. However, in about half of the analysed time periods, females formed differentiated social relationships. This indicates that factors other than dispersal patterns and within-group contest competition contribute to the formation of the ephemeral relationships, as measured by spatial proximity, among female red colobus. Therefore, our results on the patterns of female social relationships in a primate with female-biased dispersal provide important empirical insight for the refinements of theories that aim to explain social evolution in mammals.

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Group-living animals exhibit considerable variation in social structure, and the ultimate causes and consequences of this variation is a central question in behavioural ecology (Alexander, 1974; Eisenberg, Muckenhirn, & Rundran, 1972; Hinde, 1976; Möller, 2012; Schülke & Ostner, 2012). In most primates and other mammals, food resources are most crucial for the reproductive success of females but not males (Trivers, 1972; Wrangham, 1980). Thus, the distribution of food resources is considered to be more important for female compared to male reproductive strategies, and theoretical attempts to explain interspecific variability in primate social structure have focused on the link between ecological factors and female social behaviour (Clutton-Brock & Janson, 2012; Koenig, Scarry, Wheeler, & Borries, 2013; Sterck, Watts, & van Schaik,

1997; van Schaik, 1989; Wrangham, 1980). More specifically, the so-called socioecological models have focused on evolutionary and ecological explanations for variability in female feeding competition and the resulting characteristics of agonistics, or dominance, relationships (Koenig et al., 2013; Sterck et al., 1997; Wheeler, Scarry, & Koenig, 2013). In contrast, nonagonistic relationships among females (hereafter called social relationships), which are usually derived from affiliative interactions (e.g. grooming) and/or spatial proximity, are only considered implicitly in these models despite the considerable scientific interest they have received in general. Crucially, to develop and test a theoretical framework to explain variability in social relationships, it is essential to systematically assess characteristics of such relationships in a variety of group-living mammals, including species with contrasting social behaviour, ecology and other potentially important factors.

However, for primates, studies of which have been central to the development of this body of theory, detailed investigations of social

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relationships have focused on species where females remain in their natal groups (i.e. female philopatry) and frequently exchange affiliative behaviours, such as grooming. For example, numerous studies in such species have shown that closely related females within groups form strong social relationships with each other (baboons, *Papio* spp.: Seyfarth, Silk, & Cheney, 2012; Silk, Alberts, & Altmann, 2006; macaques, *Macaca* spp.: De Moor, Roos, Ostner, & Schülke, 2020; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001; capuchins, *Capucinus* spp.: Kalbitzer et al., 2017; Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008). As a consequence of this kin bias in social behaviour, female social relationships in such groups are commonly highly differentiated, stronger within matriline than across matriline (i.e. clustered) and stable over time (Kalbitzer et al., 2017; Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012). Importantly, the ability of females to form relationships with other females appears to have fitness consequence, as shown by a link between female social connectedness and infant survival and/or longevity (Archie, Tung, Clark, Altmann, & Alberts, 2014; Ellis, Snyder-Mackler, Ruiz-Lambides, Platt, & Brent, 2019; Kalbitzer et al., 2017; Ostner & Schülke, 2018; Silk, Alberts, & Altmann, 2003). Although questions about the mechanisms underlying this link remain to be answered (Ostner & Schülke, 2018; Thompson, 2019), the importance of female social relationships in such primate species appears to be well established.

In contrast, female social relationships in species with female dispersal are poorly understood. Research on chimpanzees, *Pan troglodytes* (Langergraber, Mitani, & Vigilant, 2009; Lehmann & Boesch, 2009) and black-and-white colobus, *Colobus vellerosus* (Wikberg, Ting, & Sicotte, 2014), indicate that even in species with female-biased dispersal, females can form strong, and sometimes stable, relationships with other females. However, such research is rare and primarily conducted in species where the exchange of affiliative behaviours among females is relatively frequent.

Therefore, our aim here is to investigate female social relationships in a primate with female dispersal and low rates of affiliative interactions, the endangered Ugandan (or ashy) red colobus monkey, *Piliocolobus tephrosceles*, in Kibale National Park, Uganda. These animals live in multilevel-multifemale groups where females usually disperse during or shortly after adolescence (Struhsaker, 2010). Adult females do not appear to form strong affiliative relationships as they are only rarely observed to groom each other (Struhsaker, 2010; Tombak, Wikberg, Rubenstein, & Chapman, 2019). Tombak et al. (2019) found that females only exchanged grooming once every 2 h (269 grooming bouts during 588 h of focal observations). Including additional data from ad libitum sampling, there was some evidence for reciprocal grooming patterns, but the authors did not study the general patterns of female social relationships. Thus, a more general investigation of social relationships in female red colobus is still missing.

We analysed 9 years of continuously collected data to investigate three aspects of female social relationships among female red colobus: differentiation, stability and clustering. The quantification of these characteristics can provide important insights into whether females may have preferences for other individuals at all, and, if so, what factors might be linked to such preferences. Given the low frequency of affiliative interactions in female red colobus, we established the strength of social relationships based on spatial proximity. Proximity data have been used for this purpose for a number of species, and patterns of spatial proximity are commonly correlated with grooming interactions (e.g. chimpanzees: Langergraber et al., 2009; capuchins: Kalbitzer et al., 2021; macaques: De Moor et al., 2020).

A high degree of differentiation (or variability) of social relationships indicates that individuals are preferentially associating

with a subset of other individuals (Whitehead, 2008b). This means that some dyads are characterized by strong relationships, whereas most dyads exhibit weak or no relationships. In contrast, a low degree of differentiation indicates that all relationships within a group are similar in strength. Establishing the differentiation of social relationships is crucial, because if there is no variability, there is no point in investigating the predictors or consequences of such variability. Social differentiation has been investigated in a range of nonprimate and primate species, including Trinidadian guppies, *Poecilia reticulata* (Heathcote, Darden, Franks, Ramnarine, & Croft, 2017), sperm whales, *Physeter macrocephalus* (Gero, Gordon, & Whitehead, 2015), and chacma baboons, *Papio ursinus* (Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009). Recently, Moscovice, Sueur, and Aureli (2020) formulated a comparative framework in which they suggested that one of the most important factors underlying variability in social differentiation is the extent to which individuals within a group overtly compete over resources with each other (i.e. within-group contest competition). A high degree of within-group contest competition is expected if some group members are able to monopolize resources. According to Moscovice et al. (2020), this should promote strategies to cooperate with preferred partners to monopolize access to resources, resulting in a greater differentiation of social relationships. Furthermore, they suggested that another important factor underlying variability in social differentiation is the extent to which individuals differ in their ability to provide services to others. For example, some individuals may be more effective coalition partners (e.g. high-ranking animals), provide access to more valuable information, or their tolerance at specific locations within a group is more important (e.g. positions close to high-quality food resources).

Red colobus in Kibale primarily feed on leaves (Chapman, Chapman, & Gillespie, 2002), a widely distributed resource that is not easy to monopolize, and females rarely show agonistic or coalitional behaviour (Tombak et al., 2019). This suggests that contest competition among females is low, which should, according to the framework described above, result in a low degree of social differentiation. Nevertheless, females may sometimes prefer to spend time in proximity with each other for other reasons, for example, because they are attracted to another female with a young infant (e.g. Kalbitzer et al., 2017). Therefore, we expected that female social relationships would not be consistently differentiated. Thus, we predicted that some periods would be characterized by greater social differentiation than assessed for permuted networks with randomized female–female associations, whereas other periods would be indistinguishable from these null models.

Temporal stability of social relationships indicates that individuals have long-term preferences for specific partners. Some philopatric females do not form stable social relationships with their kin (e.g. crested macaques, *Macaca nigra*; Duboscq et al., 2017), and some dispersing females form long-term relationships with nonkin (e.g. chimpanzees; Langergraber et al., 2009). However, the typical pattern in primates appears to be stable, long-term social relationships among closely related females in species where females remain in their natal groups (see above), which is presumably favoured by kin selection. Since female red colobus in Kibale disperse to other groups, we predicted that female social relationships would not be consistently stable over time. Females may show preferences to spend time in proximity to other females for a short time (e.g. to another female with an infant), but because we did not expect consistent preferences for specific partners, we predicted that the female social networks would not be consistently more stable than permuted social networks.

Finally, clustered social relationships are expected if subgroups of individuals within a group preferentially associate with each other. As for temporal stability, this is expected from populations

with female philopatry and where closely related females associate with each other in matrilineal groups. Based on the female-biased dispersal pattern in red colobus, we predicted that female social relationships would not be clustered within the group. Instead, we predicted that observed patterns of clustering within the group would be indistinguishable from permuted networks.

Various approaches have been applied to quantify these characteristics of social networks, and there is no consensus of the best method. Thus, we used several methods to derive each of these three network characteristics to provide more robust results. In addition, different methodological approaches reflect slightly different biological aspects of the same general network characteristic. For example, the temporal stability of social relationships can be investigated for the entire network or for relationships with top partners only (Silk, Cheney, & Seyfarth, 2013); thus, a comparison of these metrics can provide important insights as to which relationships are important over a long period. Therefore, our primary aim is to provide theoretical insights about social relationships in red colobus and primates in general, but we also hope to help establish a roadmap to investigate animal social structure in a variety of species. This will hopefully allow for systematic comparisons of social relationships across taxa, which will be the foundation for a better understanding of animal social evolution.

METHODS

Study Site, Group and Behavioural Data

Behavioural data were collected between December 2007 and November 2016 from a group of red colobus in Kibale National Park, Uganda (795 km²; 0°13′–0°41′N, 30°19′–30°32′E). This group ranged in the moist, evergreen forests of the Kanyawara area near Makerere University Biological Field Station (Chapman & Lambert, 2000). In this equatorial region, rainfall is bimodal with two wet and two dry seasons each year and an annual average rainfall of 1677 mm (1990–2019). The group ranged in what are locally known as Forestry Compartments K-30 and K-14. The K-30 site is a 282 ha area of old-growth forest that has never been commercially harvested, but a few large stems (0.03–0.04 trees/ha) were removed by pitsawyers before 1970. The K-14 area is a 405 ha forest block that was logged at low intensity (14 m³/ha or 5.1 stems/ha) from May through December 1969. Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage, but the area the group used was very lightly affected (Chapman et al., 2010; Chapman & Lambert, 2000; Skorupa, 1988; Struhsaker, 1999).

Two to three Ugandan field assistants, who were able to individually recognize all adults within the group, spent on average 8 days per month with the red colobus (mean \pm SD = 8.37 \pm 3.04 days, range 1–18 days). To assess individual behaviour, scan samples were recorded every 15–30 min, with the frequency depending on other data collection going on at the time. For each scan sample, the field assistants selected five adults (female or male) within clear sight. Then, they recorded for each of these five individuals, its identity, its behaviour, the identity of the nearest neighbour (NN) and the distance to this NN (there was no maximal distance, but we limited the analysis to nearest neighbours within 5 m). Seeing an animal in the complex arboreal environment with enough detail to determine its identity is often very time consuming (e.g. they do not show their faces); thus, five individuals per scan ensured the sample was not biased towards easily observable/identifiable individuals and/or a particular habitat type. Following each scan, the observers moved to another part of the group and conducted the next scan. Scans were usually recorded between 0800 and 1600 hours, and the aim was to get at least one

record per adult individual for each observation day. Once all individuals were sampled on a given day, the field assistants started the next round of scan samples with the goal of sampling all individuals within the group. The aim of this approach was to include observations of all individuals within the group for a comparable number of times per day, and to specifically search for and record individuals in the periphery of the group to prevent bias towards central individuals.

All fieldwork was strictly observational and the researchers kept sufficient distance to the habituated monkeys to prevent any disturbance of their activities. No signs of distress or disturbance was noticeable from the monkeys during observations. Permission to conduct the research was given by the Uganda National Council for Science and Technology and the Uganda Wildlife Authority, and the procedures, which were limited to observations of habituated animals, were approved by McGill University's Animal Care Committee (MUACC No. 5041).

Sample Description

For our social network analysis, we combined our scan data into 3-month and 6-month periods resulting in 36 and 18 consecutive time periods, respectively. Three-month periods are the minimum length of time to include most adult females for each of the time periods in our analysis following the criteria outlined below (for the number of included females during each period, see below and Appendix, Table A1). We also considered 6-month periods to evaluate whether the scarcity of social data affected our results. We decided against the analysis of periods longer than 6 months because such periods would have been more likely to include changes in social relationships within rather than between consecutive periods and, therefore, prevented us from detecting changes in differentiation, stability or clustering of social relationships.

Over the 9 years, the number of adults in the group ranged from 28 to 36 females and from 11 to 19 males (Appendix, Table A1). Over the study, there were 65 different adult females and 41 different adult males in the group. From each scan, we only kept records where an adult female was recorded with another adult female as nearest neighbour and applied the following criteria: we excluded all females that were observed fewer than five times in total as an adult either with another adult female as NN, or as an NN of another adult female within 5 m. At the dyadic level, we excluded pairs of females where the sum of observations of female A plus observations of female B while both were adult and present in the group (but not necessarily nearest neighbours) was less than 5. We applied these two rules to ensure that we had at least some information about each female and dyad so that association indices (see below) were not heavily affected by the small number of observations. The number of excluded females was very low in relation to the total number of females, ranging from 0 to 4 (mean \pm SD = 0.556 \pm 0.843) for the 3-month periods, and 0 to 1 (mean \pm SD = 0.333 \pm 0.485) for the 6-month periods (see Appendix, Table A1 for details). After applying these rules, we were able to include 13 250 different scan samples for the 3-month period analysis, recorded on 848 days, and containing 24 626 records of adult females with another adult female as NN within 5 m (Appendix, Table A1). For the analysis using 6-month periods, we included 13 332 scan samples, recorded on 854 days, containing 24 801 dyadic records of adult females.

Social Relationships

We assessed social relationships between individuals within each time period based on spatial proximity by calculating an

association index using the following procedure: we calculated for each female i the number of times she was observed as an adult while female j was present in the group as an adult (observed _{i,j}). Thus, for each dyad, the sum of observed _{i,j} and observed _{j,i} is the maximum number of times the two females i and j could have been observed together while both were adult (hereafter d_{ij}).

Then, we determined the number of times individual j was recorded as the NN of individual i (NN _{i,j}). Thus, the sum of NN _{i,j} and NN _{j,i} is the number of times these two adults were actually observed together while both were adult (hereafter x_{ij}). Based on these numbers, we calculated an association index for each dyad ij comparable to the simple ratio index (SRI; Whitehead, 2008a):

$$\text{SRI}_{ij} = \frac{\text{NN}_{i,j} + \text{NN}_{j,i}}{\text{Observed}_{i,j} + \text{Observed}_{j,i}} = \frac{x_{ij}}{d_{ij}} \quad (1)$$

Thus, SRI _{ij} is the ratio of how often the two individuals were observed together as nearest neighbours in relation the number of times they could have been observed together. This index therefore represents an undirected estimate of the strength of social relationships, based on nearest neighbour information from both individuals, and corrected for adult co-residence time in the group.

Differentiation of Social Relationships

As there is no consensus about how to assess different social network characteristics, we used two common approaches to assess the differentiation of social relationships for our female red colobus social networks (Table 1). (1) The calculation of the coefficient of variation of all SRI _{ij} values (hereafter CoV_{SRI}). This metric is defined as the ratio of the standard deviation to the mean (σ/μ), in this case, SRI _{ij} values, and therefore represents a standardized measure of how variable observed social relationships are within a group or community (for examples, see Heathcote et al., 2017; Henzi et al., 2009; Kalbitzer et al., 2017; Leu, Farine, Wey, Sih, & Bull, 2016). (2) The estimate of social differentiation (S) as suggested by Whitehead (2008a, 2008b). He argued that in the context of social differentiation it is important to distinguish between the observed (α) and the true association index (α'), because the variance of α (here: CoV_{SRI}) is a combination of the variance of α' and the sampling variance. Following his suggestion, we used a maximum likelihood approach to separate these sources of variation and estimate 'the coefficient of variation in the true association index' (i.e. the CoV of α' labelled as S ; for examples, see Gero et al., 2015; Kovacs, Perrtree, & Cox, 2017). According to Whitehead (2019), values below 0.3 indicate rather homogeneous societies and values above 0.5 indicate well-differentiated societies. The calculation is detailed in Method A1 (Appendix).

Stability of Social Relationships

We assessed the stability of social relationships between consecutive time periods t_1 and t_2 by calculating two metrics (Table 1). (1) The Kendall rank correlation coefficient (τ) for temporally adjacent networks (t_1 and t_2), including SRI _{ij} values for all dyads (hereafter $\tau_{t_1 t_2}$). With this procedure we tested whether the ordering (or ranking) of the strength of dyadic social relationships was similar between two consecutive time periods. (2) The partner preference index (PPI), as suggested by Silk et al. (2013), which reflects whether the identities of top partners (with regard to relationship strength) remain the same over time. We calculated the PPI from one time period to the next for all females and then averaged these values as a global measure of female partner preference (hereafter PPI _{$t_1 t_2$}). In contrast to $\tau_{t_1 t_2}$, this index focuses on the stability of social relationships with top partners instead of all relationships with all partners, because in some animals the strongest relationships that an individual forms may be biologically more important than the weaker relationships (Silk et al., 2013). We here considered between one and four top-partners. Details for the calculation of $\tau_{t_1 t_2}$ and PPI _{$t_1 t_2$} are provided in Method A2 (Appendix).

Clustering of Social Relationships

To assess the degree of female social clustering within each time period, we assessed three different metrics, the last two of which are based on the same algorithm (Table 1). (1) The global weighted clustering coefficient (CC; Barrat, Barthélemy, Pastor-Satorras, & Vespignani, 2004), which indicates the proportion of an individual's partners that are connected with each other, averaged for all individuals in the network and weighted by the strength of their relationships (SRI _{ij}). (2) The scaled clustering ratio (SCR), which reflects the number of detected clusters (or modules) by the 'Louvain' network community detection algorithm (as implemented in the igraph package; Csardi & Nepusz, 2006) in relation to individuals within a group. We scaled this metric from 0 to 1, so that a value of 0 indicates that all females were put into the same cluster and a value of 1 indicates that each female was put into its own cluster. (3) The modularity for each network based on the detected clusters. This metric indicates the strength of connections within clusters in relation to connections between clusters and, therefore, how useful the estimated clustering is to describe the division within a group or population (Whitehead, 2008a). In a social network with a high modularity, individuals primarily interact within their own clusters, whereas in a network with a low modularity, individuals interact at similar frequencies within and across clusters. These three metrics all reflect slightly different aspects of social clustering within a group. Details for the calculation of CC, SCR and modularity are provided in Method A3 (Appendix).

Table 1
Assessed network characteristics and calculated metrics

Social network characteristic	Metric	Description
Differentiation of social relationships	CoV _{SRI}	Coefficient of variation of the simple ratio association index (SRI _{ij})
	S	Maximum likelihood estimates of the variation of the 'true association index' using the number of times dyads that were observed together (x_{ij}) and the maximum number of times each dyad could have been observed together (d_{ij} ; for details see Method A1)
Stability of social relationships	$\tau_{t_1 t_2}$	Kendall rank correlation coefficients (τ) for temporally adjacent matrices with SRI _{ij} values (see Method A2)
	PPI _{$t_1 t_2$}	Average partner preference index calculated for top 1, 2, 3 and 4 partners based on SRI _{ij} values (Method A2)
Clustering of social relationships	CC	Weighted clustering coefficient based on SRI _{ij} values (Method A3)
	SCR	Scaled clustering ratio of number of clusters detected by Louvain algorithm per individual based on SRI _{ij} values (Method A3)
	Modularity	Connection strength within vs between clusters using clusters detected by Louvain algorithm based on SRI _{ij} values (Method A3)

For details, see Methods in the main text and the Appendix.

Permutation Procedure to Create Null Distributions

Observations of different individuals within a network are not independent of each other, and, therefore, violate this assumption of most statistical procedures. Furthermore, differences between individuals in how data were collected are often unavoidable (e.g. number of observations, temporal pattern of observations) and this can introduce patterns easily misinterpreted as social structure (Farine, 2017). Thus, the construction of null models is an important consideration when testing hypotheses about social network structure. For social network analysis, a common approach (e.g. Gero et al., 2015; Heathcote et al., 2017; Langergraber et al., 2009) is to apply permutation procedures that result in a null distribution of networks with features of the original structure but where associations among individuals are the result of randomly interacting individuals (i.e. individuals that show no preferences to associate with specific other individuals). The observed networks can then be compared to these null distributions of permuted networks.

Here, we applied a pre-network permutation procedure to construct our null distributions, because this approach is more efficient in decreasing rates of both false positives (type I errors) and false negatives (type II errors) compared with null models created by network (or node) permutations (Farine, 2017; but see Weiss et al., 2021 with regard to the application of this type of permutation for regression models). For this procedure, we randomly swapped nearest neighbours within each time period to obtain permuted networks with randomized associations between females. Thus, the number of observations per individual remained the same, but potentially existing preferences to spend time in the proximity to other individuals within the group were removed. These permuted networks were then used to obtain null distributions for all of our metrics described above (CoV_{SRI}, S , τ_{112} , PPI₁₁₂, CC, SCR and modularity). The details of this procedure are described in Method A4 (Appendix).

For all of these null distributions of our social network metrics, we calculated the 80%, 90% and 95% percentile intervals (PI₈₀, PI₉₀, PI₉₅), which we compared to the values obtained from observed networks. Furthermore, for each metric and time period, we derived P values based on these randomized networks by combining the observed with randomized values and then ranking all of these values from small to large (hereafter rank_{observed}). Tied values obtained average ranks (thus, two identical values on the sixth and seventh rank would get a rank of 6.5). Then, we calculated a one-sided P value $p_{1_perm} = \text{rank}_{\text{observed}} / \text{number of values}$. If this value was > 0.5 , we used $p_{1_perm} = 1 - p_{1_perm}$. To obtain a two-sided P value (hereafter p_{perm}), we simply multiplied this value by 2.

Since we calculated each of these metrics for a large number of networks (one for each time period), multiple testing would be an issue for formal null hypothesis significance testing. However, we took a different approach, because our aim was not to derive binary decisions for each metric and time period, and because approaches used to correct for multiple testing as well as the threshold used for P values to be considered sufficient evidence for rejecting a specific null hypothesis vary. We discuss our p_{perm} values in combination with the observed effect sizes and consider the generally observed temporal pattern, number of comparisons and sample sizes.

RESULTS

There was considerable variation in the strength of social relationships among dyads. For the analysis of 3-month periods, SRI_{ij} values ranged from 0 to 0.400, and mean values ranged from 0.018 to 0.036. For the analysis of 6-month periods, the distribution was similar, and SRI_{ij} ranged from 0 to 0.391, and mean values ranged

from 0.018 to 0.031. Network densities (i.e. the proportion of connected dyads in relation to all dyads) ranged from 0.317 to 0.766 for the 3-month period analysis and from 0.624 to 0.855 for the 6-month analysis. The average number of associations observed per individual (H) and per time period ranged from 3.96 to 32 for the 3-month periods (mean \pm SD = 18.4 \pm 5.39; note that all values were above 10 except for the period starting on 1 March 2013) and from 15.2 to 51.6 for the 6-month periods (mean \pm SD = 35.6 \pm 8.05).

Differentiation of Social Relationships

Female red colobus formed differentiated social relationships during some, but not all, of the time periods. Considering S for 6-month periods as an indicator of social differentiation, the observed values ranged between 0.27 and 0.51 (mean = 0.41; Fig. 1; also see Appendix, Table A2). For nine out of 18 periods, the observed S fell outside the PI₉₅ of S values based on permuted networks, and during all but one of these nine periods, p_{perm} was < 0.001 (Appendix, Fig. A1b). Thus, according to S values, there was evidence that half of the periods were characterized by socially differentiated networks.

The PI₉₅ bands were relatively variable over time (Fig. 1a, Appendix, Table A2). As a consequence, absolute values of S were not necessarily indicative of whether the value fell outside the PI₉₅. For example, the S value for the period starting on 1 December 2011 was similar or even larger than S values for the six periods starting on or after 1 December 2013 (Fig. 1a). However, the first value of S was within the PI₉₅ ($p_{perm} = 0.070$), whereas all of the S values for the latter six periods clearly fell outside the PI₉₅ bands (all $p_{perm} < 0.001$).

A visual inspection of the social network for a period with a high (Fig. 1b) and a low (Fig. 1c) value of S indicates that during periods of high differentiation, a few dyads formed strong relationships, but most dyads formed weak relationships. In contrast, all dyads in networks with low differentiation formed weak relationships.

Result for the analysis with the 3-month periods were very similar to the results with the 6-month periods. If the S value for at least one of the two 3-month periods overlapping with a 6-month period indicated differentiated social relationships, the S value for the 6-month periods suggested the same (Appendix, Fig. A1a, b).

The CoV_{SRI} values were generally larger than the S values for the 6-month periods, ranging from 0.71 to 1.11 (mean = 0.91; Appendix, Table A2). However, comparing observed CoV_{SRI} values with the PI₉₅ bands led to similar conclusions about which networks were differentiated or not. More specifically, some, but not all, of the periods were characterized by differentiated female social networks. For example, observed CoV_{SRI} values for eight of the 18 6-month periods were outside the PI₉₅ bands. Five of these eight periods were also socially differentiated according to S , but only three showed strong evidence for social differentiation ($p_{perm} < 0.001$; one p_{perm} value was < 0.01 , and the remaining four values were between 0.025 and 0.05, which would not be considered as significant following usual corrections for multiple testing).

The correlation between the true and the estimated association indices, which can be approximated by calculating the ratio between S and CoV, is a measure of how well the estimated association indices (here SRI_{ij}) describe the social structure of a community (Whitehead, 2008b). For our observations from female red colobus, this ratio ranged from 0.27 to 0.57 (mean \pm SD = 0.46 \pm 0.08) for 6-month periods and from 0.01 to 0.53 (mean \pm SD = 0.38 \pm 0.11) for the 3-month periods (see Appendix, Fig. A2; note that the lowest ratio of 0.01 was observed in the time period starting 1 March 2013, where we also had by far the lowest average number of observed associations per individual, H ; see Results). Thus, the 6-month

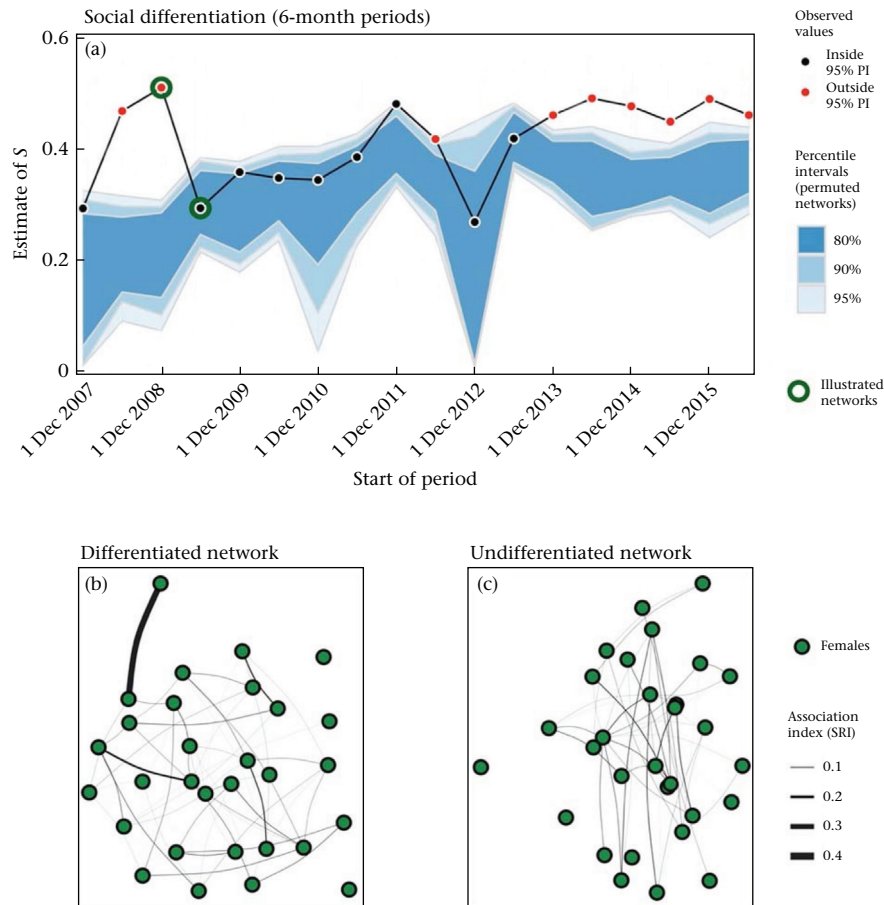


Figure 1. Differentiation of social relationships in female red colobus in Kibale National Park, Uganda. (a) Changes in differentiation of social relationships (S) in observed networks versus permuted networks is shown for 6-month intervals. The red dots indicate observed S values outside the 95% percentiles based on permuted networks (PI_{95}). Social network diagrams (sociograms) are shown for (b) a 6-month period for a highly differentiated network and (c) a lowly differentiated network. The observed S values for these two networks are indicated in (a) by encircled points. For more details, see [Appendix, Fig. A1](#).

periods were generally a better representation of female red colobus social structure than the 3-month periods.

Stability of Social Relationships

Our assessment of the temporal stability of social relationships indicated that female red colobus rarely formed lasting relationships with each other, and only some relationships appeared to be stable over short periods. Considering τ_{t1t2} for the 17 pairs of temporally adjacent 6-month periods, these coefficients indicated no temporal correlation of social relationship strength (range 0.06–0.21, mean = 0.15; [Fig. 2a](#), [Appendix, Table A2](#)). Furthermore, only one of these τ_{t1t2} values fell outside the PI_{95} band ([Fig. 2a](#); the value for the period from 1 December 2012 to 1 June 2013), but the respective value of 0.16 indicated only a very weak correlation, and the p_{perm} value of 0.040 indicated that it was not very unlikely to find this value by chance given the number of compared periods. In comparison, the shorter 3-month periods resulted in a slightly larger range of τ_{t1t2} values with lower minimum and greater maximum values (range 0.01–0.21, mean = 0.11; [Appendix, Fig. A3a](#), [Table A2](#)). For 12 out of the 35 comparisons of adjacent 3-month periods, τ_{t1t2} values were outside the respective PI_{95} band, but for only three of these values, p_{perm} values of < 0.001 indicated strong evidence for τ_{t1t2} values that were larger than expected by chance. Furthermore, these τ_{t1t2} values only indicated a weak

correlation of social relationships between time periods (range 0.15–0.21).

The PI_{95} bands for τ_{t1t2} values for 3-month and 6-month periods were highly variable over time (see [Fig. 2a](#), [Appendix, Fig. A3a, b](#)), and some PI_{95} bands were not overlapping at all with each other (e.g. the PI_{95} for the 6-month time period starting on 1 December 2012 versus the PI_{95} for the period starting on 1 December 2013).

These patterns were largely confirmed by the assessment of the PPI_{t1t2} . Using 6-month periods and evaluating the PPI_{t1t2} for the top three partners, values ranged from 0.05 to 0.21 (mean 0.14; [Appendix, Table A2](#)), indicating a very low stability of relationships with top partners. Furthermore, only 2 out of 17 observed PPI_{t1t2} values fell outside the PI_{95} band. Very similar patterns were observed considering 3-month periods and the top one, two, three and four partners ([Appendix, Fig. A4a–h](#)). In general, PI_{95} were relatively stable over time ([Appendix, Fig. A4a–h](#)).

Clustering of Social Relationships

Female red colobus did not form social clusters. For the 6-month periods, observed CC values ranged from 0.66 to 0.91 (mean = 0.82; [Appendix, Table A2](#)), and none of these values was above the PI_{95} band based on permuted networks ([Fig. 3a](#)); however, three out of 18 values were below the respective PI_{95} . For the 3-month periods ([Appendix, Fig. A5a](#)), observed CC values were slightly lower than

for 6-month periods (range 0.34–0.83; mean = 0.68; Appendix, Table A2) and 2 out of 36 the CC observed values were below the PI_{95} . The PI_{95} bands for 3-month and 6-month periods were highly variable over time (Fig. 3a, Appendix, Fig. A5a, b, Table A2).

The values of the SCR for 6-month periods ranged from 0.07 to 1 (mean = 0.5), but the values were either close to 0 or equal to 1. This means that the algorithm either assigned females to very few clusters (SCR close to 0) or each female was assigned to her own cluster (SCR = 1). This pattern was identical for the PI_{95} band, and none of the SCR values fell outside the respective PI_{95} . These results were largely supported the analysis of 3-month periods (Fig. A5e–f).

Modularity values for 6-month periods were generally low and ranged from 0 to 0.11 (mean = 0.05; Fig. 3c, Appendix, Table A2). Modularity was always 0 for networks with a maximum number of clusters (i.e. SCR = 1) because, under such circumstances, there was a single female per cluster, and social relationships within clusters cannot exist. Only 2 out of 18 values were outside the PI_{95} band, with strong evidence for one of these values being larger than by chance ($p_{perm} < 0.001$). For 3-month periods, values ranged from 0 to 0.17 (mean = 0.09; Appendix, Fig. A3e, Table A2); thus, the upper bound was slightly larger, but the pattern was similar to the 6-month periods. Observed modularity values for 3 out of 36 time periods fell outside the PI_{95} , two of which had $p_{perm} < 0.001$.

The PI_{95} bands for 3-month and 6-month periods were highly fluctuating over time.

DISCUSSION

In species or populations where females remain in their natal group (i.e. female philopatry), they often form strong, long-term relationships (commonly called ‘bonds’) with their kin (Kalbitzer et al., 2017; Silk, Altmann, & Alberts, 2006; Silk et al., 2012), which leads to patterns of differentiated, stable and clustered relationships within their social networks. Observations from primates with female-biased dispersal indicate that differentiated and temporarily stable relationships among females can exist as well (Langergraber et al., 2009; Lehmann & Boesch, 2009). However, studies on such species with female-biased dispersal, and specifically on primates with low frequencies of female affiliative interactions, remain very scarce.

Red colobus in Kibale represent a population where females disperse from their natal groups and affiliative (and agonistic) interactions are rare (Struhsaker, 2010; Tombak et al., 2019). Our results generally confirm the expected pattern of social structure for such a population: despite analysing 9 years of continuous data, we did not detect strong evidence for the formation of stable social relationships among females. Furthermore, there was no indication of social clusters within our group, which would be expected if females prefer to associate with their kin (i.e. matriline). Finally, our observations mostly support the predictions by Moscovice et al. (2020) for a primate without intense within-group contest competition and presumably little variability among females to provide services to other females (such as coalitionary support). For

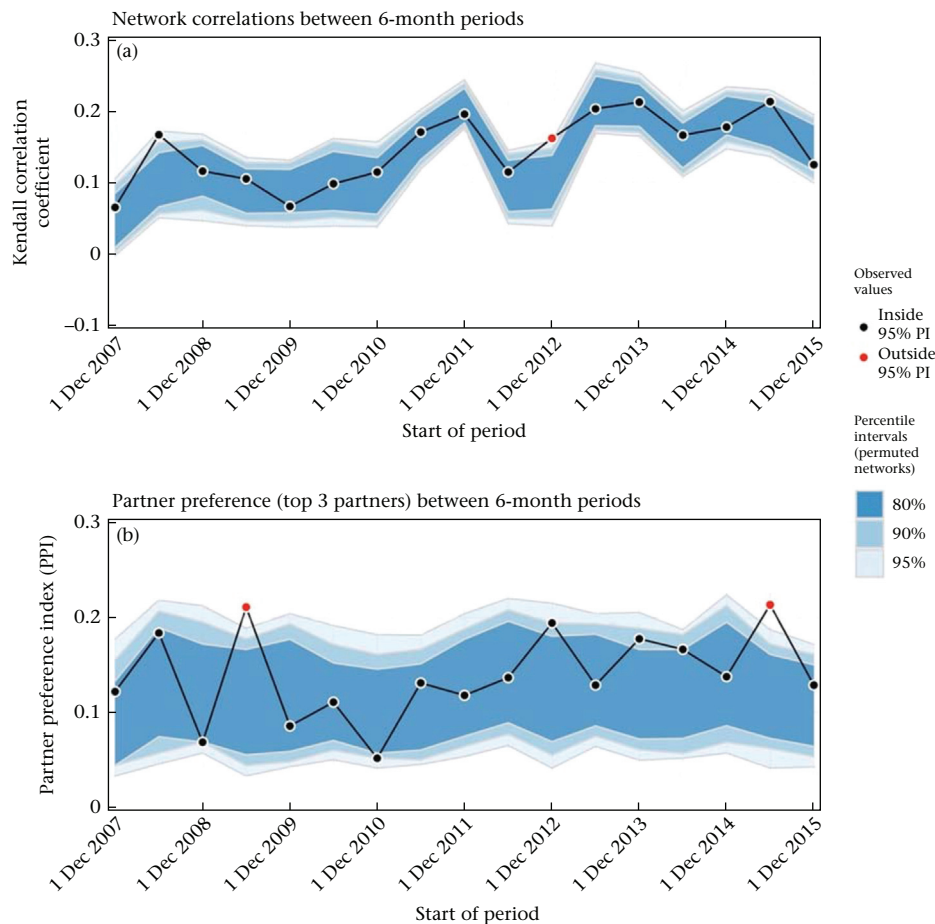


Figure 2. Temporal stability of social relationships of red colobus in Kibale National Park, Uganda assessed by (a) the Kendall rank correlation coefficient (τ_{112}) and (b) the partner preference index (PPI_{112}) for adjacent 6-month periods.

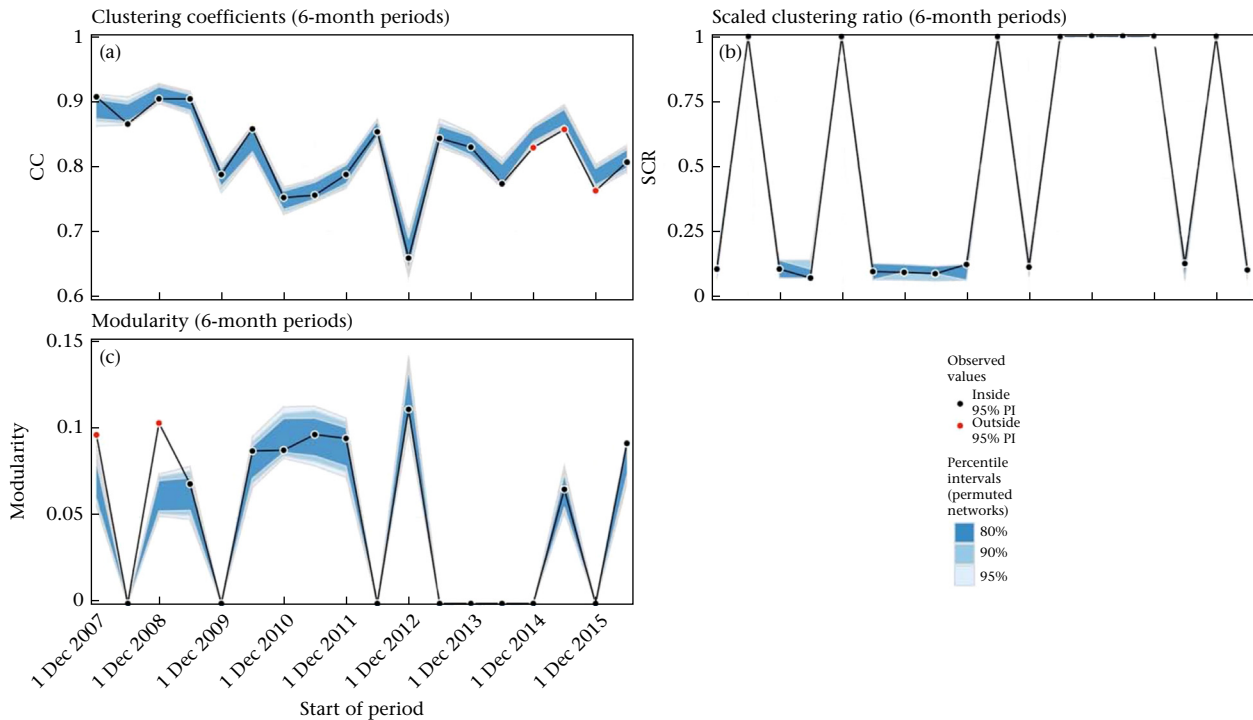


Figure 3. Clustering of social relationships in female red colobus in Kibale National Park, Uganda according to (a) global clustering coefficients (CC), (b) relative number of clusters per individual (SCR) and (c) modularity analysed for 6-month periods.

about half of the time periods, there was no indication of social differentiation, and during most (but not all) of the other periods, the degree of social differentiation appeared to be relatively small.

As pointed out above, even in species with female-biased dispersal, females can show well-differentiated and long-lasting preferences for other females, as observed for chimpanzees in Taï National Park, Cote d'Ivoire (Lehmann & Boesch, 2009), or in Kibale National Park in Uganda (Langergraber et al., 2009). To better understand the evolution of social behaviour in mammals, it is important to investigate which factors are linked to these differences in social behaviour between species and populations with similar dispersal patterns. In line with the arguments made by Moscovicce et al. (2020), Lehmann and Boesch (2009) speculated that in Taï chimpanzees, the formation of strong and stable social relationships among females, even nonkin, are important because they exhibit a relatively high degree of intense contest competition. This makes it beneficial for females to form such relationships to receive support during agonistic encounters over food resources. In contrast to Taï chimpanzees, however, the degree of female contest competition in red colobus in Kibale appears to be low (Tombak et al., 2019). Thus, dispersal patterns might explain the general tendencies for the formation of female social relationships in primates, but under some circumstances, other factors, such as diet and the distribution of resources, may make the formation of strong social relationships even with nonkin important.

Even in female red colobus, networks of some of the 3-month periods were weakly correlated with the temporarily adjacent networks, which indicates that some dyads may have maintained stable associations over short periods. Furthermore, about half of the networks were characterized by a degree of social differentiation that was larger than expected by chance, with estimates of S ranging from ~ 0.4 to ~ 0.6 . According to Whitehead (2019), values below 0.3 indicate rather homogeneous societies, whereas values above 0.5 indicate well-differentiated societies. According to this

categorization, female red colobus sometimes formed well-differentiated social relationships and some of these relationships appeared stable over short periods. While this pattern is clearly different from the pattern described for some of the well-investigated primate species with female philopatry (e.g. most baboons, or macaques), it is crucial to understand the factors that are linked to such rather subtle variability in female social networks.

It is important to consider that behavioural adaptations occur over evolutionary timescales, and animals may lack the flexibility to respond to changes in current ecological conditions, even if such responses would be beneficial (i.e. phylogenetic constraints; Chapman & Rothman, 2009; Di Fiore & Rendall, 1994). As a result, some predictions based on ecological variability may be accurate within clades, but phylogenetic constraints prevent animals from showing the expected responses at a larger, between-clade, scale (Koenig et al., 2013). Thus, while the general pattern in the social structure of female red colobus in Kibale may be constrained to what is expected for a species with female dispersal and a generally low intensity of food contest competition, the observed subtle temporal changes are possibly explained by ecological variability at a short timescale. Furthermore, the effect of such ecological variability on social networks may interact with interindividual differences in behavioural strategies. For example, some females may temporarily have the same preferences for a location or food resource (e.g. similar dietary needs experienced by lactating females), and, as a consequence, may associate with each other more often than expected by chance.

Variability in the distribution and availability of food will lead to temporary changes in the potential for feeding contest competition, and subtle behavioural responses to this change may be reflected in the social structure of the group. For example, in chacma baboons, *Papio ursinus*, strength, variability (as assessed by the CoV) and clustering of social relationships varies between periods of food

abundance and food scarcity (Henzi et al., 2009). Although female red colobus usually feed on widely available leafy food resources (Chapman et al., 2002), they nevertheless seem to prefer young leaves, often found at the top of canopy, of specific tree species (Ganzhorn, 1995; Rothman, Chapman, & Van Soest, 2012). Thus, the availability and spatial distribution of such preferred young leaves may be related to the observed temporal changes in social differentiation in red colobus.

Social relationships are also likely crucial with regard to anti-predatory strategies. For example, under experimental conditions, Trinidadian guppies form more stable and differentiated social relationships when the perceived predation risk is high, perhaps because efficient antipredatory strategies rely on cooperation among individuals (Heathcote et al., 2017). Furthermore, predators often ambush from the edges of groups, and for some species, such as white-faced capuchin monkeys, *Cebus imitator* (Hall & Fedigan, 1997; Kalbitzer et al., 2017), or vervet monkeys, *Chlorocebus pygerythrus* (Josephs, Bonnell, Dostie, Barrett, & Henzi, 2016; Teichroeb, White, & Chapman, 2015), spatial centrality has been used as a proxy for safety from predators. Thus, social structure in red colobus, which are sometimes depredated by chimpanzees, may also change in response to perceived predation pressure. In addition, different individuals may vary in their response to such environmental changes, which may also result in the emergence of differentiated social relationships. For example, Trinidadian guppies with similar scores of shyness/boldness prefer each other (Croft et al., 2009), and the strength of such assortments may manifest depending on predation pressure. Similarly, captive chimpanzees with similar scores of sociability and boldness also preferred each other (Massen & Koski, 2014), and this may also be more relevant during periods of higher predation pressure (or feeding competition).

A commonly raised concern for social network analyses is whether sample sizes are sufficiently large to detect the expected patterns, because even in groups with a small number of individuals, the number of potential relationships (or 'edges') can be very large (Davis, Crofoot, & Farine, 2018). For this reason, we applied various approaches to ensure that our conclusions were reasonable: (1) we analysed 3-month and 6-month periods because we were concerned that the sample sizes for some of the shorter periods may have been too small to detect important features of their social structure. If that were case, we would have expected to observe changes in the resulting patterns between the 3-month and 6-month analysis; however, our conclusions were very similar for both analyses; (2) the densities of our networks were relatively high, ranging from 0.624 to 0.855 for the 6-month analysis (see results). This means that observed relationships were relatively 'spread out' within the group, supporting the conclusion that females do not have strong preferences for other individuals. Furthermore, based on a comparison of different sampling regimes to determine network structures, Davis et al. (2018) argued that small sample sizes often capture the real network structure because only a few observations are required to detect the main, or strongest, edges in a network; (3) for some of the metrics, values not only fell consistently within the 95% percentile intervals of permuted networks, these values were also fairly small considering their absolute values. For example, the correlation coefficients for consecutive networks were very low (range 0.01–0.21), making it unlikely that we missed strong temporal consistency in social relationships; (4) our comparison of S and CoV indicated that at least the analysis of the 6-month periods provided a useful representation of the social structure of female red colobus in Kibale (see Whitehead, 2008b). Thus, we view that our results reflect the major patterns of female social relationships in red colobus in Kibale.

The reason why we calculated different metrics for the same features of social networks was to improve the robustness of our results, to include metrics reflecting different aspects of the same social network characteristic and to help establish a roadmap for interspecific comparisons of social structure by providing data that can be more easily compared with studies on other species. This also revealed methodological insights, a detailed discussion of which is beyond the scope of this study, but we here mention two of the highlights.

First, despite considerable differences in the absolute values of S and CoV_{SRI} and well-reasoned criticism of the application of the CoV in this context (Whitehead, 2008b), these two metrics lead to similar conclusions about which periods were characterized by differentiated social relationships. However, there were some periods where S , but not CoV_{SRI} , indicated social differentiation, and vice versa (Appendix, Fig. A1). Thus, our results illustrate the importance of carefully interpreting the CoV, which has been used in various studies to assess social differentiation (Heathcote et al., 2017; Henzi et al., 2009; Kalbitzer et al., 2017; Leu et al., 2016).

Second, with regard to social clustering, observed values for all calculated metrics (CC, SCR, modularity) generally fell within the range of Pl_{95} bands, indicating that female red colobus do not form social clusters. However, the CC for 6-month periods was generally close to 1 because over such periods a majority of individuals were observed associating at least once with each other and, therefore, had association indices (SRI_{ij}) above 0. Although the weighted CC accounts for the strength of social relationships, it is equal to 1 if all partners are connected (Barrat et al., 2004). Thus, for social networks with a very high density, as found in many primates, the weighted CC might be of limited use and modularity may be generally better suited for such investigation. However, despite some testing with simulated data before deciding to use the Louvain algorithm to calculate modularity, we observed some issues (the 'jumping' of the number of detected clusters; see Fig. 3b), and more extensive testing of different cluster detection appears to be required before using this algorithm, or other cluster detection algorithms, to investigate social structure in animal societies.

Conclusion

Our study supports the idea that dispersal patterns and the type and intensity of feeding competition are important for the social structure of female primates. The variability in differentiation and stability of social relationships over time that we detected highlights the importance of long-term data to derive conclusions about the social structure in animal societies (Chapman, Corriveau, Schoof, Twinomugisha, & Valenta, 2017; Clutton-Brock & Sheldon, 2010). Furthermore, this variability indicates that female red colobus show flexibility in their social behaviour, and it will be crucial to investigate other factors that contribute to the formation of social relationships. Our observations on social relationships in a female-dispersed primate therefore provide important empirical insight for the refinements of theories aiming to explain social evolution in mammals.

Declaration of Interest

We declare no conflicts of interest.

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Appendix

Method A1

Calculation of S

We followed Whitehead (2008a, 2008b) to distinguish between the observed (a) and the true association index (a'). As he suggested, we used the method of maximum likelihood to estimate 'the coefficient of variations in the true association index' (i.e. CoV of a' , or S), using the following formula:

$$L = \prod_{ij} \int_0^1 \alpha'_{ij}^{x_{ij}} \times (1 - \alpha'_{ij})^{(d_{ij}-x_{ij})} \times B(\alpha'_{ij}\beta_1\beta_2) \times d(\alpha'_{ij}) \quad (A1)$$

The two shape parameters of the beta distribution B are defined as $\beta_1 = \mu \times ((1 - \mu)/(\mu \times S^2) - 1)$ and $\beta_2 = (1 - \mu) \times ((1 - \mu)/(\mu \times S^2) - 1)$. Thus, this equation allows to estimate S and μ of the true association index (a') based on the number of times dyad were observed together (x_{ij}) and the maximum number of times dyads could have been observed together (d_{ij} ; see equation 1). In contrast to the other metrics, this procedure is therefore calculated based on x_{ij} and d_{ij} and not the simple ratio index (SRI $_{ij}$). We implemented the numerical integration and likelihood maximization in R v.3.6.1 (R Core Team, 2019).

Method A2

Calculation of τ_{t1t2} and $PPI_{i,t1t2}$

Since we used undirected simple ratio indices values (SRI $_{ij}$) for all dyads (i.e. we did not distinguish between the relationship from i to j and from j to i), we had one symmetrical matrix of SRI $_{ij}$ values for each time period (i.e. the values above the diagonal of the matrix contained the same information as the values below the diagonal). Thus, to calculate the Kendall rank correlation coefficient between two consecutive time periods t_1 and t_2 (τ_{t1t2}) we only included SRI $_{ij}$ values from one side of the diagonal from each matrix. Furthermore, we only included values for dyads that were present during both time periods. Then, we applied the Kendall method (using the function 'cor.test' with argument 'method = kendall' in R) to test whether the ordering (or ranking) of the strength of dyadic social relationships was similar between two consecutive time periods. We only used this procedure to obtain correlation coefficients and derived P values from a pre-network permutation procedure described in Network Permutations.

For the second approach, we calculated the individual partner preference index ($PPI_{i,t1t2}$) for all individuals i present in t_1 and t_2 , as suggested by Silk et al. (2013):

$$PPI_{i,t1t2} = \frac{2T - U}{2T - T - X} \quad (A2)$$

Here, T is defined as the number of evaluated top-ranked partners (labelled S in Silk et al., 2013). For example, if the top two partners (i.e. the two partners with the highest SRI $_{ij}$) are evaluated, T would be 2. U is the sum of distinct top partners observed during the two time periods t_1 and t_2 and X is the number of top partners in t_1 that were not present in t_2 . Thus, this index accounts for changes in group composition and ranges from 0 (individual had the maximum number of possible top partners) to 1 (individual had the minimum number of different top partners). Thus, in contrast to the correlation test above, this index focuses on the stability of social relationship with the top partners T and not the entire network. We calculated this index for all individuals present in both t_1 and t_2 , and used $T = 1, 2, 3$ and 4 as the number of top partners. For each pair of adjacent time periods t_1, t_2 and for each T , we then calculated the average $PPI_{i,t1t2}$ over all individuals i as a global measure of female partner preference.

Method A3

Calculation of CC, SCR and Modularity

The clustering coefficient (CC) indicates the proportion of partners that are connected with each other. As a local measure,

this index ranges from 0 (none of the social partners of an individual are connected to each other) to 1 (all of the social partners are connected to each other; see, e.g. Brent, 2015). For our study, however, we were interested in clustering within the entire network and therefore used the global (average) CC. Furthermore, we used a weighted version of this coefficient (Barrat et al., 2004) using the SRI_{ij} values as weights to account for differences in the strength of social relationships (for an example, see Henzi et al., 2009). For the calculation of CC, we used the function 'transitivity' from the igraph package v.1.2.4.1 (Csardi & Nepusz, 2006).

Then, we applied a network community detection algorithm to detect potential social clusters within each of the networks. We used the 'Louvain' algorithm (Blondel, Guillaume, Lambiotte, & Lefebvre, 2008) as implemented in the function 'cluster_louvain' from the igraph package. There are many different algorithms available to detect cluster structure within networks, and many of them are implemented in igraph. Here, we chose the Louvain method because we performed preliminary tests with simulated networks comparable to our observed networks that indicated that this was one of the best performing algorithms to recover simulated clusters.

Based on the results from this algorithm, we calculated scaled clustering ratio (SCR) values, which we defined as the ratio of detected clusters to the number of individuals in a group (i.e. the maximum number of clusters). We scaled this index from 0 to 1 to make it comparable over time:

$$SCR = \frac{\text{Detected clusters} - 1}{\text{Individuals} - 1} \quad (A3)$$

Thus, a value of 0 indicates that all individuals were put into the same cluster and a value of 1 indicates that each individual was put into its own cluster.

Finally, we determined the modularity for each clustering, which indicates the strength of connections within clusters in

relation to connections between clusters and therefore how useful the estimated clustering is to describe the division within a group or population (Whitehead, 2008a). We used the igraph function 'modularity', which applies the method described by Clauset, Newman, and Moore (2004) to calculate the modularity based on the network matrix and the individual cluster memberships detected by 'cluster_louvain'.

Method A4

Network permutation procedure

We applied a pre-network permutation procedure to construct our null distributions for each time period using the following steps:

- (1) We randomly selected a record of an individual (Ind_1) from our scan data within the specified period and checked whether Ind_1 was an adult female at the time of data collection (t_1).
- (2) In the next step, we checked whether the nearest neighbour (NN_1) was within 5 m of Ind_1 and an adult female at t_1 . If these conditions were met, we proceeded to step 3; if not we went back to step 1.
- (3) Then, we randomly selected a second row for Ind_2 from the scan data within the same time period following the same procedure as above (Ind_2 and NN_2 adult females at t_2 and NN_2 within 5 m of Ind_2). If this was the case, we proceeded to 4; if not we repeated step 3 until all conditions were met.
- (4) Following that, we controlled whether NN_1 was adult and present at t_2 , and NN_2 was adult and present at t_1 . If this was the case, we swapped NN_1 and NN_2 ; if not, we went back to step 3.

For each time period, we conducted this procedure 12 000 times, thus we swapped 12 000 NNs in total. Then, we discarded the first 2000 iterations to ensure that randomized networks were

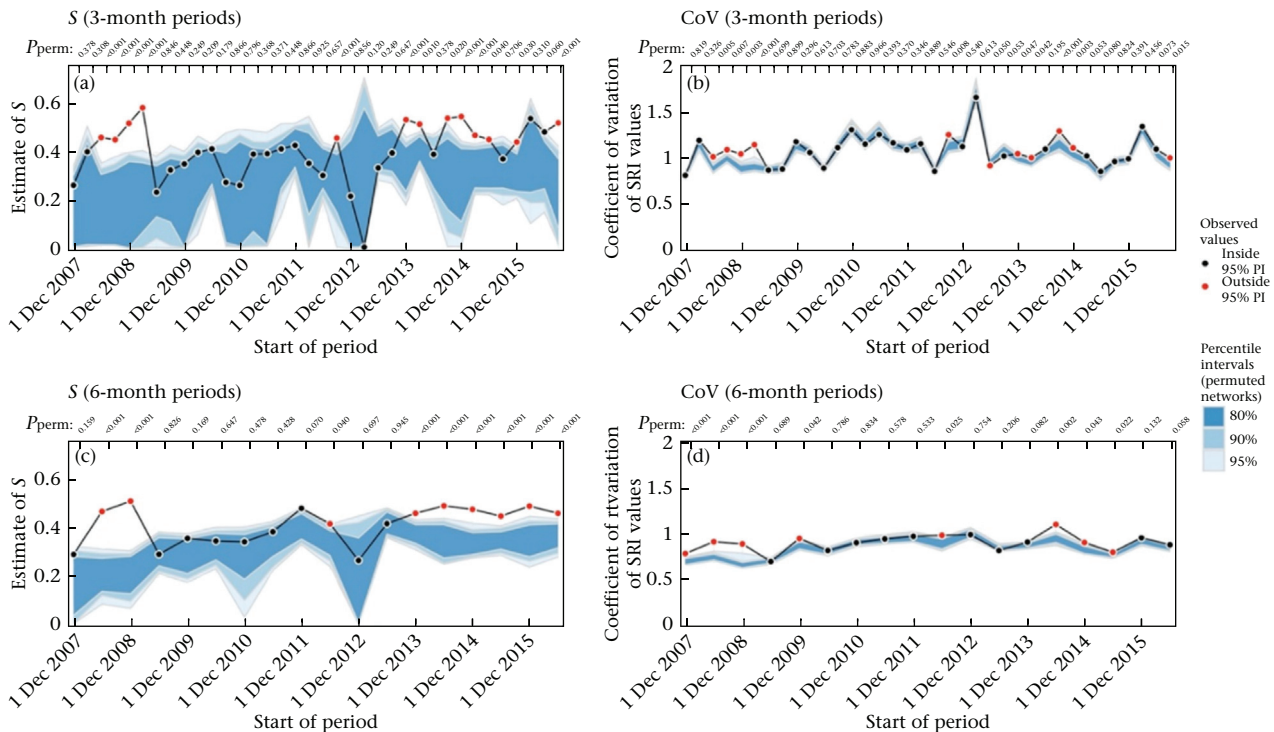


Figure A1. Changes in social differentiation in female red colobus networks over time assessed by the estimate of social differentiation (S) for (a) 3-month periods and (b) 6-month periods and by the coefficient of variation (CoV) for (c) 3-month periods and (d) 6-month periods.

sufficiently different from original networks. These permuted networks were used to obtain null distributions for all of our metrics described above (CoV_{SRI}, S , τ_{t1t2} , PPI_{t1t2}, CC, SCR and modularity).

To derive these null distributions, we kept every 10th iteration of these 10 000 networks. This means that each of the evaluated networks was 10 swapped NNs different from the previous one and the null distribution for each metrics was

based on 1000 permuted networks. However, for the calculation of the null distribution of S , we only kept every 50th iteration because the likelihood maximization and associated numerical integration required for S can consume considerable computational time. Nevertheless, the null distributions for S were based on 200 permuted networks, which should be a good indication of how this metric is distributed given random associations among females.

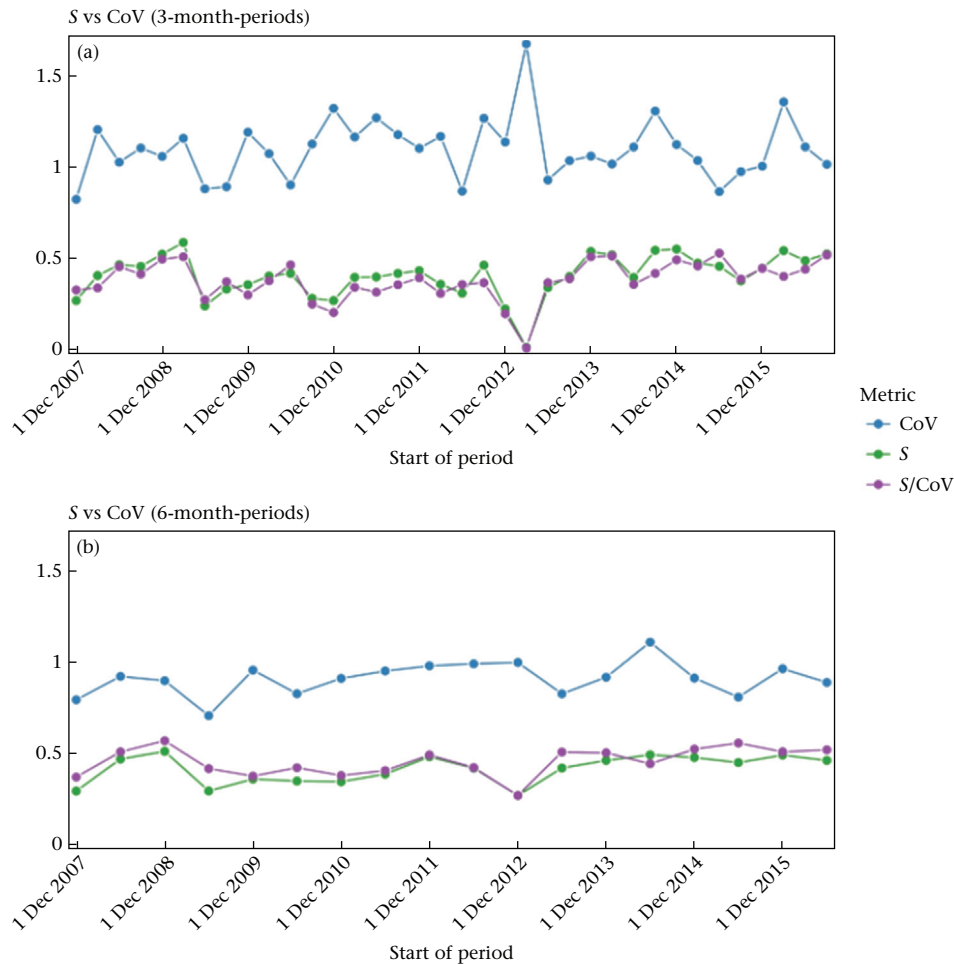


Figure A2. Comparison of the estimate of social differentiation (S) and the coefficient of variation (CoV) for (a) 3-month periods and (b) 6-month periods.

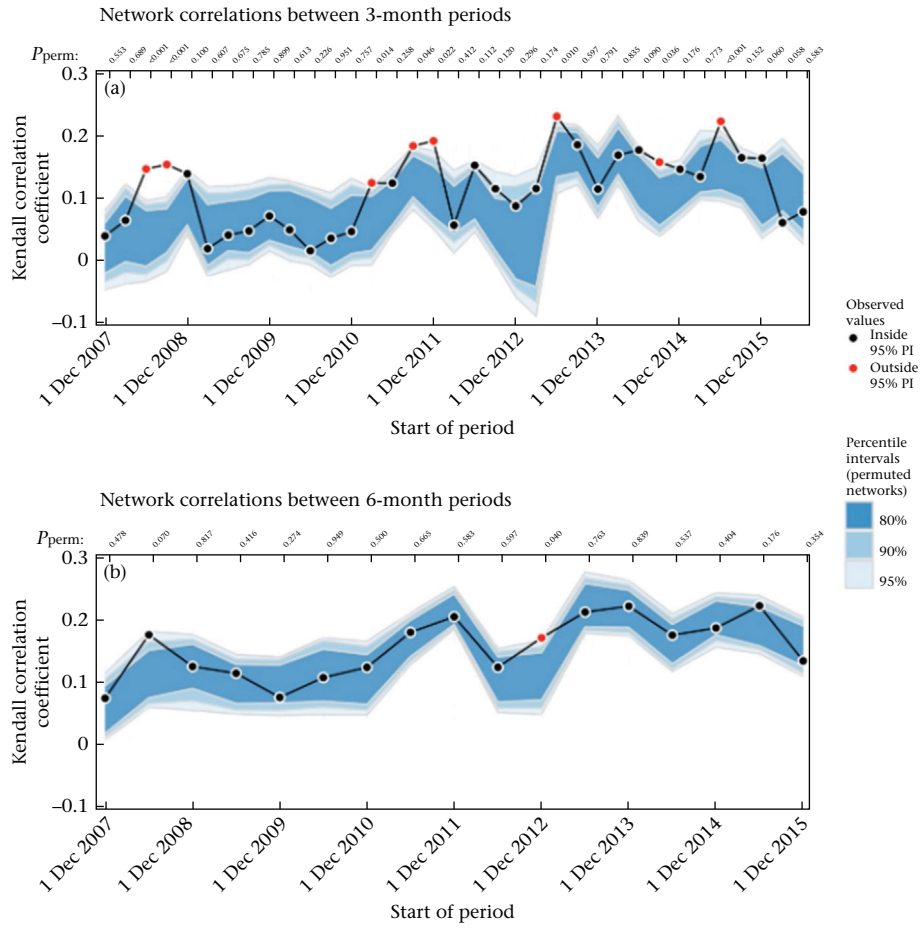


Figure A3. Stability of social relationships assessed by matrix correlations for (a) 3-month periods and (b) 6-month periods.

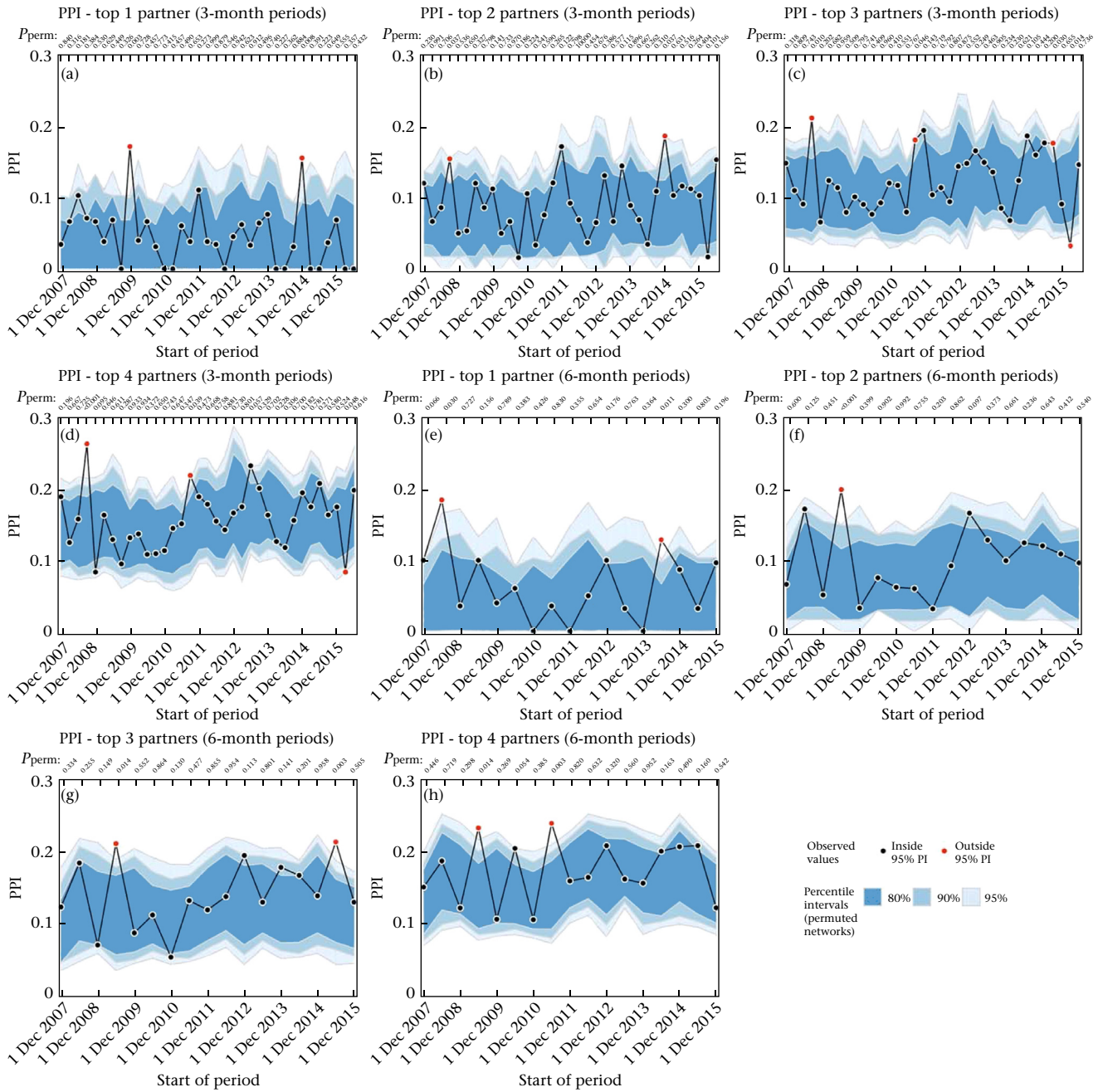


Figure A4. Stability of social relationships assessed by the partner preference index for one to four top partners and (a–d) 3-month periods and (e–h) 6-month periods.

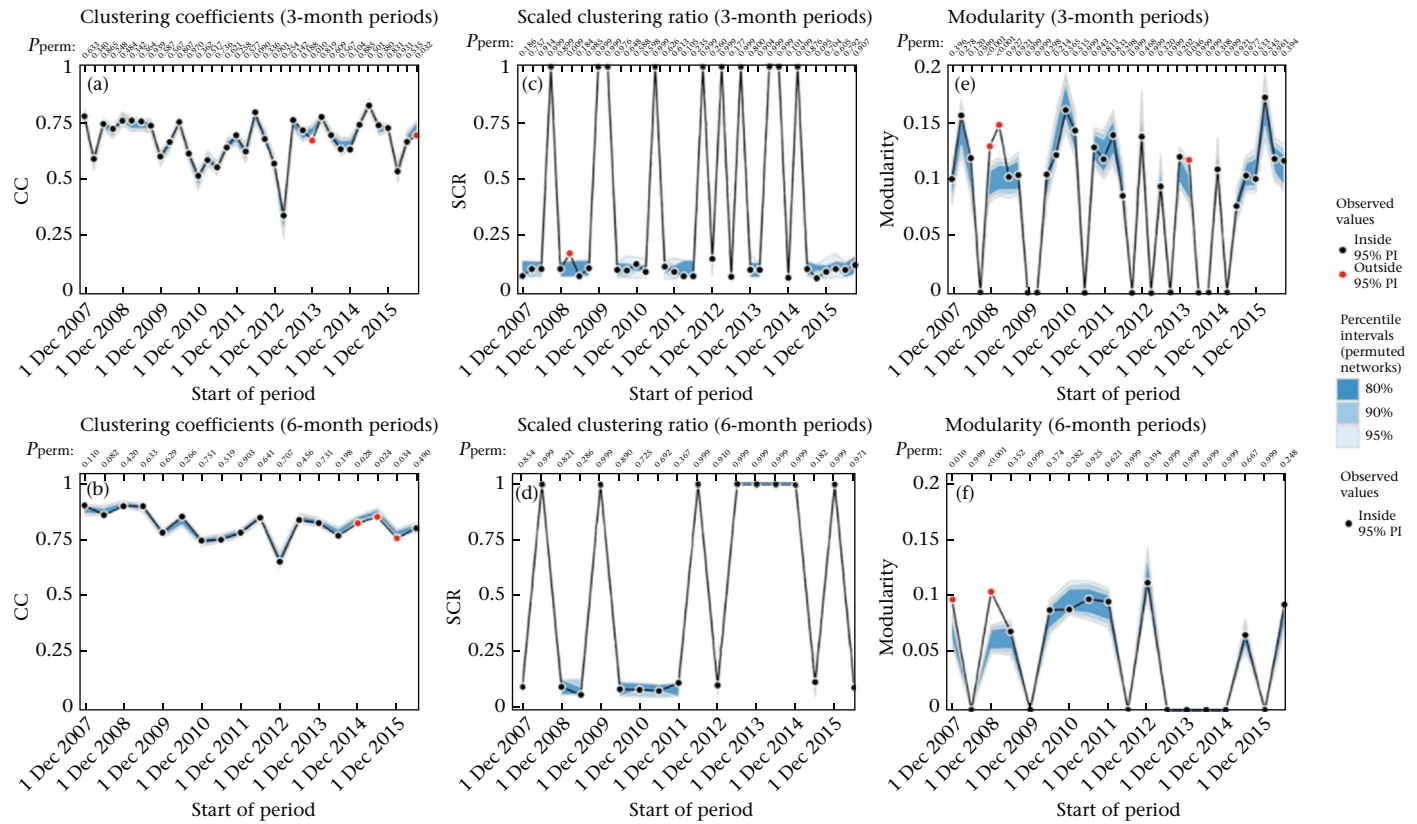


Figure A5. Social clustering in female red colobus monkeys as indicated by the clustering coefficient for (a) 3-month and (b) 6-month periods, relative to the number of clusters per individual (SCR) for (c) 3-month and (d) 6-month periods and modularity for (e) 3-month and (f) 6-month periods.

Table A1

Group composition and sample sizes during the study period

Time intervals			Group size (adults)		Sample size			
Length	Start	End	Females	Males	Females	Days	Scans	Records
3 months	1 Dec 2007	29 Feb 2008	30	16	29	26	327	736
	1 Mar 2008	31 May 2008	30	14	30	16	179	394
	1 Jun 2008	31 Aug 2008	31	15	30	29	340	666
	1 Sep 2008	30 Nov 2008	31	13	31	29	316	603
	1 Dec 2008	28 Feb 2009	30	13	30	30	362	742
	1 Mar 2009	31 May 2009	30	13	30	30	358	731
	1 Jun 2009	31 Aug 2009	31	13	29	28	303	702
	1 Sep 2009	30 Nov 2009	30	14	29	32	336	682
	1 Dec 2009	28 Feb 2010	33	13	32	25	260	515
	1 Mar 2010	31 May 2010	34	11	34	30	328	723
	1 Jun 2010	31 Aug 2010	32	12	32	23	485	950
	1 Sep 2010	30 Nov 2010	33	14	33	20	385	722
	1 Dec 2010	28 Feb 2011	34	14	33	16	318	594
	1 Mar 2011	31 May 2011	34	14	34	21	389	728
	1 Jun 2011	31 Aug 2011	35	14	34	17	274	531
	1 Sep 2011	30 Nov 2011	36	14	36	18	406	854
	1 Dec 2011	29 Feb 2012	35	17	35	24	436	866
	1 Mar 2012	31 May 2012	31	17	30	12	248	472
	1 Jun 2012	31 Aug 2012	32	18	29	24	434	844
	1 Sep 2012	30 Nov 2012	32	18	32	23	392	712
	1 Dec 2012	28 Feb 2013	28	17	28	12	218	370
	1 Mar 2013	31 May 2013	29	16	24	4	72	127
	1 Jun 2013	31 Aug 2013	32	19	31	26	457	753
	1 Sep 2013	30 Nov 2013	31	18	31	22	420	663
	1 Dec 2013	28 Feb 2014	31	18	31	26	420	703
	1 Mar 2014	31 May 2014	31	16	31	31	547	913
	1 Jun 2014	31 Aug 2014	31	17	31	24	366	616
	1 Sep 2014	30 Nov 2014	33	15	32	20	353	590
	1 Dec 2014	28 Feb 2015	32	15	32	22	389	682
	1 Mar 2015	31 May 2015	34	15	34	30	563	1011
	1 Jun 2015	31 Aug 2015	31	17	31	32	589	1054

Table A1 (continued)

Time intervals			Group size (adults)		Sample size			
Length	Start	End	Females	Males	Females	Days	Scans	Records
6 months	1 Sep 2015	30 Nov 2015	33	17	33	33	518	863
	1 Dec 2015	29 Feb 2016	34	18	34	30	560	940
	1 Mar 2016	31 May 2016	33	17	32	14	212	372
	1 Jun 2016	31 Aug 2016	32	17	31	24	369	659
	1 Sep 2016	30 Nov 2016	28	17	27	25	321	543
	Entire study period		65	41	65	848	13250	24626
	1 Dec 2007	31 May 2008	30	16	30	43	520	1170
	1 Jun 2008	30 Nov 2008	32	15	32	58	656	1269
	1 Dec 2008	31 May 2009	30	13	30	60	720	1473
	1 Jun 2009	30 Nov 2009	31	15	30	61	646	1403
	1 Dec 2009	31 May 2010	35	13	35	55	588	1238
	1 Jun 2010	30 Nov 2010	33	14	33	43	870	1672
	1 Dec 2010	31 May 2011	34	14	34	37	707	1322
	1 Jun 2011	30 Nov 2011	37	14	36	35	680	1385
	1 Dec 2011	31 May 2012	35	18	35	37	701	1378
	1 Jun 2012	30 Nov 2012	33	19	32	47	826	1556
	1 Dec 2012	31 May 2013	29	17	28	16	290	497
	1 Jun 2013	30 Nov 2013	33	19	32	49	892	1440
	1 Dec 2013	31 May 2014	34	18	34	58	988	1656
	1 Jun 2014	30 Nov 2014	34	17	33	44	719	1206
1 Dec 2014	31 May 2015	34	18	34	52	952	1693	
1 Jun 2015	30 Nov 2015	34	17	34	65	1107	1917	
1 Dec 2015	31 May 2016	35	19	35	44	772	1312	
1 Jun 2016	30 Nov 2016	32	18	31	50	698	1214	
Entire study period		65	41	65	854	13332	24801	

'Scans' refer to the total number of scans included into the analysis, and 'Records' refer to the number of records where an adult female was observed with another adult female as nearest neighbour during these scans.

Table A2
Variability in observed metrics and metrics calculated from permuted networks

Metric	Period length (months)	Observed value			Permuted networks								
					Median		2.5% Percentile		97.5% Percentile		PI 95% range		
		Min	Max	Mean	Min	Max	Min	Max	Min	Max	Min	Max	Mean
CoV _{SRI}	3	0.82	1.67	1.1	0.81	1.71	0.77	1.58	0.87	1.88	0.09	0.3	0.13
	6	0.71	1.11	0.91	0.67	1.01	0.63	0.95	0.75	1.08	0.07	0.17	0.11
S	3	0.01	0.58	0.4	0.05	0.44	0.01	0.34	0.34	0.71	0.14	0.7	0.37
	6	0.27	0.51	0.41	0.18	0.42	0.01	0.36	0.31	0.48	0.12	0.44	0.21
CC	3	0.34	0.83	0.68	0.3	0.84	0.24	0.81	0.36	0.86	0.04	0.13	0.06
	6	0.66	0.91	0.82	0.67	0.91	0.63	0.9	0.7	0.93	0.03	0.07	0.04
SCR	3	0.06	1	0.35	0.09	1	0.06	1	0.12	1	0	0.1	0.06
	6	0.07	1	0.5	0.09	1	0.06	1	0.11	1	0	0.07	0.04
Modularity	3	0	0.17	0.09	0	0.17	0	0.14	0	0.19	0	0.06	0.03
	6	0	0.11	0.05	0	0.12	0	0.1	0	0.14	0	0.04	0.02
τ_{r1t2}	3	0.01	0.22	0.11	0.01	0.17	-0.1	0.11	0.07	0.22	0.1	0.24	0.13
	6	0.06	0.21	0.15	0.04	0.21	0	0.18	0.11	0.27	0.07	0.12	0.1
PPI _{r1t2} (4 partners)	3	0.08	0.26	0.16	0.12	0.18	0.06	0.11	0.19	0.29	0.12	0.2	0.15
	6	0.1	0.24	0.17	0.12	0.18	0.07	0.12	0.2	0.25	0.12	0.17	0.14
PPI _{r1t2} (3 partners)	3	0.03	0.21	0.12	0.09	0.14	0.03	0.07	0.15	0.25	0.11	0.22	0.15
	6	0.05	0.21	0.14	0.09	0.14	0.03	0.07	0.17	0.22	0.13	0.17	0.15
PPI _{r1t2} (2 partners)	3	0.02	0.19	0.09	0.06	0.09	0	0.02	0.12	0.22	0.12	0.22	0.16
	6	0.03	0.2	0.1	0.05	0.1	0	0.03	0.14	0.2	0.11	0.19	0.15
PPI _{r1t2} (1 partners)	3	0	0.17	0.05	0	0.05	0	0	0.09	0.18	0.09	0.18	0.13
	6	0	0.19	0.06	0	0.05	0	0	0.09	0.18	0.09	0.18	0.14