Temporal patterns in the social network of core units in Rwenzori Angolan colobus monkeys: effects of food availability and inter-unit dispersal

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Abstract

Multi-level societies are complex social systems where basic core units associate in a hierarchical manner, allowing animals to adjust group size in response to local conditions. Each tier of multi-level societies may have evolved under different selective pressures and understanding the effect of temporal variation in these pressures may help determine why these types of social systems form. Our goal was to examine the degree of temporal variability in inter-unit associations in a multi-level society of Rwenzori Angolan colobus monkey (Colobus angolensis ruwenzorii), and to determine whether social or ecological factors correlated with association patterns. Using social network analyses, we described the association patterns of 12-13 core units over 21-months and investigated the effect of changes in rainfall, food availability, and inter-unit dispersals. We found that core unit networks were denser and more clustered when fruit was abundant, likely due to reduced food competition. Male dispersals also occurred more at these times, suggesting that greater band cohesion allowed males to prospect for dispersal opportunities. Within the band, we observed the formation of an all-male unit and the transfer of one core unit between clans. Our findings highlight how ecological conditions can influence association patterns, interunit relationships, and ultimately social organization.

INTRODUCTION

Complex, hierarchical social systems, termed multi-level societies, are present in species from many distantly related taxa, such as birds (Papageorgiou et al., 2019), cetaceans (Whitehead et al., 2012), equids (Rubenstein & Hack, 2004), proboscideans (Wittemyer, Douglas-Hamilton, & Getz, 2005), primates (Grueter, Matsuda, Zhang, & Zinner, 2012), and chiropterans (Kerth, Perony, & Schweitzer, 2011). Determining why these types of societies evolve and how they function are key questions in biology. In multi-level societies, stable subgroups (hereafter core units) associate in a hierarchical manner (Grueter, Qi, Li, & Li, 2017). Up to four tiers of non-random association have been documented, with higher tiers numbering hundreds of individuals in some species (Grueter, Matsuda, Zhang, & Zinner, 2012; Snyder-Mackler, Beehner, & Bergman, 2012; Schreier & Swedell, 2012a; Wittemeyer et al., 2005). The factors that determine the number and composition of different social tiers and the ways that ecological and social pressures affect their stability are still poorly understood for most species (Grueter et al., 2017; Farine et al., 2015).

Several hypotheses have been proposed to explain the function of different tiers in multi-level societies. The advantages and disadvantages of group living for animals have been well documented (Krause & Ruxton, 2002) and multi-level societies appear to have evolved because they allow animals to adjust group size more fluidly than is possible in stable groups (Aureli et al., 2008; Grueter et al., 2017). Large aggregations are beneficial, primarily because of the multiple ways that they lower predation risk (i.e., detection, dilution,

1

predator confusion, defence, Hamilton, 1971; Pulliam & Caraco, 1984), while the chief cost of large group size is the increase in food competition that results from many conspecifics together (Terborgh & Janson, 1986). Indeed, there are examples of multi-level societies forming large aggregations at higher tiers when predators are nearby (e.g., *Papio hamadryas*, Schreier & Swedell, 2012b; *Physeter microcephalus*, Whitehead et al., 2012), and fissioning to lower tiers when resource availability is reduced (e.g., *Loxodonta africana*, Wittemyer et al., 2005; *Orcinus orca*, Foster et al., 2012; *Papio hamadryas*, Schreier & Swedell, 2012b; *Rhinopithecus roxellana*, Qi et al., 2014). An alternative explanation for the evolution of multi-level societies, the bachelor threat hypothesis (Rubenstein, 1986), has garnered support, particularly in zebras and primates (e.g., Rubenstein & Hack, 2004; Pappano, Snyder-Mackler, Bergman, & Beehner, 2012; Xiang et al., 2014). This hypothesis suggests that core units (which are one-male/multi-female (OMUs) in many species) associate to decrease the amount of harassment they receive from extra-unit males (Grueter & van Schaik, 2009; Rubenstein, 1986).

In addition to predation, food competition, and conspecific threat, the degree that animals associate can be influenced by breeding seasonality (Baden, Webster, & Kamilar, 2016), migration (Colbeck et al., 2013), genetic structure (kinship) (Reisinger, Beukes, Hoelzel, & de Bruyn, 2017), and phylogeny (Balasubramaniam et al., 2018). Some of these factors fluctuate over time, often in a predictable, seasonal manner that can lead to adjustments in association patterns as animals try to balance the costs and benefits of group living. Thus, to understand if and how temporal environmental changes influence tier formation in multi-level societies, it is important to study social behaviour over time, both within and between the social tiers (Grueter, Chapais, & Zinner, 2012). Primates are good study subjects to examine the various factors influencing tier formation and stability in multi-level societies because researchers are often able to collect detailed observational data on many identifiable individuals.

Our goal was to determine the degree of temporal variability in inter-unit associations in a recently discovered multi-level society of Rwenzori Angolan colobus monkey (*Colobus angolensis ruwenzorii*), and to determine which social and ecological factors may influence this variability. This multi-level society, described for our population at Lake Nabugabo, Uganda, is unique among primates in that it contains not only OMUs, but also core units that are multi-male/multi-female (MMUs), with up to eight socially-integrated, reproductive males (Stead & Teichroeb, 2019). There are at least three tiers of social organization; core units fission and fuse with one another throughout the day but associate preferentially with core units from the same clan and clans share a home range in a band tier of organization. Initial cluster analyses with one year of data revealed two clans in our study band of 12 core units (Stead & Teichroeb, 2019). We do not yet know the selective pressures that influence tier formation or if tiers are stable over time.

In this study, we applied social network analysis (SNA) to core unit associations observed over 21 months at Nabugabo. SNA has proven extremely useful in elucidating the form of multi-level societies (e.g., Papageorgiou et al., 2019; Snyder-Mackler et al., 2012; Zhang, Li, Qi, MacIntosh, & Watanabe, 2012) and determining how within-unit interactions structure them (Matsuda et al., 2012). Further application of SNA to understanding the associations between the higher tiers in multi-level societies offers a view of the dynamics of these complex social systems (Yeager, 1991). We first examined whether clan-level groupings of *C. a. ruwenzorii* core units stayed the same over time. Unlike many other social orders of mammals, primates tend to form stable groups over relatively long periods of time that are structured by the bonding of the philopatric sex (Altmann et al., 1996; Silk, 2001; 2002; Di Fiore, 2012). These kin-based systems extend beyond the smallest social unit to higher tiers in primate multi-level societies (Colmenares, 2004; Snyder-Mackler, Alberts, & Bergman, 2014; Morrison, Groenenberg, Breuer, Manguette, & Walsh, 2019). Preliminary data thus far suggest that though both males and females disperse from their natal core unit in *C. a. ruwenzorii*, and males transfer into other core units within the band while most females emigrate out of the band (Stead & Teichroeb, 2019). Thus, male kinship could structure relations between core units, leading to stable clans over time. Second, we examined temporal variation in core unit clustering relative to ecological (seasonality in rainfall and food availability) and social (inter-unit dispersals) conditions. Greater overall food availability should allow larger aggregations to form because food competition is alleviated (e.g., Foster et al., 2012; Schreier & Swedell, 2012b; Wittemyer et al., 2005). This temporal clustering of groups

due to resource availability may then allow individuals to assess dispersal opportunities in other groups (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009; Mares, Bateman, English, Clutton-Brock, & Young., 2014), which could potentially lead to a seasonal pattern in dispersals (e.g., Ekernas & Cords, 2007; Yao et al., 2011; Young et al., 2019). In addition, groups that have recently had individuals disperse between them may associate more closely during these periods compared to when no transfers are occurring; likely because it takes time for bonds among former group members to sever and to establish bonds in the new group (Isbell & Van Vuren, 1996).

Accordingly, we hypothesized that both ecological and social variables (i.e., male relationships) would influence clan stability and the degree of clustering among *C. a. ruwenzorii* core units. We predicted that clans would be stable over time, due to tolerance of close proximity between core units that share male kin or familiar males. Fruits are the only food type positively selected for and these are high in quality compared to the rest of this species' diet, which consists largely of young leaves (JAT, unpubl. data). We therefore predicted that core unit clustering would be influenced most strongly by the availability of fruits, and that core units would associate more during times of high fruit availability when food competition is minimized. We further predicted that greater clustering of core units at times of peak fruit availability, would allow males to assess the possibilities for immigration in other core units, leading to a seasonal pattern of dispersal between core units. Finally, we predicted that associations between core unit dyads would be more frequent during and immediately after male transfer between them.

Methods

Study Species and Site

This study was conducted on a population of wild Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*) (aka Adolf Friedrich's Angolan colobus) located in a forest fragment near Lake Nabugabo, Masaka District, central Uganda (0°22'-12°S and 31°54'E). Lake Nabugabo is a small lake (8.2 x 5 km) west of Lake Victoria surrounded by a mix of swamp, wetland, grassland, primary and secondary forest, and degraded patches of forest (Chapman et al., 2016). This study focused on a band (TR band) of 132-139 colobus in 12-13 core units including one all-male unit (Stead & Teichroeb, 2019), occupying a moist tropical forest fragment made up partly of the Manwa Forest Reserve (~280 ha) lying on the west side of Lake Nabugabo (Teichroeb, Bridgett, Corriveau, & Twinomugisha, 2019). The forests that the study band occupies are at a mean elevation of 1,151 m with a relatively flat terrain (range: 1,134 – 1,167 m). Annual rainfall in this area during the Aug. 2017- July 2018 period was 758.59 mm across two rainy seasons, one from February to May and another from September to November. The mean annual temperature was 22.2°C (min. 18.7°C, max. 26.2°C) (Adams & Teichroeb, 2020). The three most dominant tree species in the forest, in terms of both stem number and basal area, are *Pseudospondias microcarpa* (Anacardiaceae), *Maesopsis eminii* (Rhamnaceae), and *Funtumia latifolia* (Apocynaceae) (Teichroeb et al., 2019).

Data Collection

Core unit associations were recorded during behavioural follows conducted over 21 months between August 28th, 2017 and May 13th, 2019 (243 days) by two trained field assistants (E. Mujjuzi and H. Kakeeto). From August 28th, 2017 to Aug. 22nd, 2018, 12 core units were sampled and from Aug. 29th, 2018 to May 13th, 2019, 13 units were sampled because it became obvious that an all-male unit (AMU) had formed by the splitting off of seven adult males from the largest core unit (Lovoa), which subsequently became an OMU that was markedly less cohesive than the other units. We deemed 21 continuous months of data as sufficient to answer our questions because four rainy seasons were covered and clans had sufficient time to change in core unit membership. One focal unit was followed each day between 8:00 h -16:00 h and all individuals were identified based on physical characteristics (e.g., broken fingers, tail shape, nipple colouration). Scan samples on core unit association were taken every two-hours, where the number and identity of core units within a 50 m radius of the focal core unit was recorded along with the time and date (overall $N = 907$ scans). We chose a two-hour interval between scans to help ensure their independence. We reasoned that two hours was enough time for core units to shift their position relative to one another (Stead & Teichroeb,

3

2019). Our data collection regime led to a relatively even distribution of focal days among core units during the study (mean N days/unit = 20.17, range: 14-25; mean N scans/unit =75.25, range: 56-90). Dispersals of individuals within the study band were recorded on notice of occurrence and a date range during which the dispersal occurred was generated based on the last time an individual was noted in their original core unit. The month of dispersal was determined to be the month with the most potential dates within that range.

To examine the seasonality of association patterns, we considered three ecological variables: rainfall, the availability of young leaves, and the availability of fruits. Rainfall data (mm per month) was obtained from https://www.worldweatheronline.com/masaka-weather-history/masaka/ug.aspx for the nearby town of Masaka (12.5 km away). We considered the availability of young leaves and fruits as these food items comprise the majority of the *C. a. ruwenzorii* diet at this field site (96%, JAT, unpubl. data). Food availability indices were calculated for each of these plant parts, for each month of the study period. We used a line-transect survey to estimate tree species abundance (i.e., number of trees and their basal area) within the home range of the *C. a. ruwenzorii* band. Thirty-two parallel transects set 100 m apart were cut throughout a 140 ha section of the forest and all trees >10 cm DBH within 5 m of either side of the transect were identified and measured (covering 9.702 ha) (Teichroeb et al., 2019). The seasonal availability of these plant parts was estimated using monthly phenology surveys of 126 trees of 44 species that were known to be consumed by*C. a. ruwenzorii*. During phenology surveys, observers indexed the percent canopy cover of mature vs. young leaves, ripe and unripe fruit, ripe and unripe seed pods, and buds vs. flowers in at least three sample trees of each species. We calculated the food availability index for both young leaves and fruits separately by multiplying the mean monthly phenology score for each plant part in each of the 44 species by the total basal area of that species, and summing these values for all the tree species consumed (Dasilva, 1994; Fashing, 2001; Saj & Sicotte, 2007).

Cluster Analyses and Preferred Associations

To determine if the clustering of core units into clans was consistent over time we used SOCPROG (v.2.9: Whitehead, 2009) and split the data into two sampling periods to compare metrics by year: August 28th, 2017 – August 22nd, 2018 (sample period 1) and August 29th, 2018 – May 13th, 2019 (sample period 2). We created an association matrix for each year by calculating the simple association index of each dyad, where a value of 1 indicates the two core units were always in association and 0 indicates they were never in association. The simple association index (AI) was chosen because we were always able to positively identify all core units in association with the focal unit (Whitehead, 2008). AI was calculated as $AI = N_{AB}/ (N_A + N_B)$ or the number of times that two core units were in association during scans, divided by the total number of scans where either unit was present. Of four different clustering methods (average linkage, Ward's weighted, complete linkage, and single linkage), the average linkage method had the highest cophenetic correlation coefficient (CCC = 0.891), so this was the clustering method that we used for hierarchical cluster analyses (see Stead & Teichroeb, 2019). We used dendrograms (Fig.2) created through the average linkage method to compare clustering into clans between sample periods. Previous work examining the graph of cumulative bifurcations from the dendrogram from sample period one showed one significant knot at an AI of 0.05 (Stead & Teichroeb, 2019), so this was the cut-off that we used to determine clan associations. We then conducted permutation tests for preferred/avoided associations using SOCPROG, and permuted association matrices 10,000 times to stabilize p-values. The network may not be static throughout the sample periods, and thus the results of this test could not reveal the variability within each sample period. Further analyses using smaller time windows was performed to adjust for this.

Smaller Time-Window Comparisons

We used the R package netTS (Bonnell & Vilette, 2019), that makes use of time-aggregated windows to analyse temporal changes in social networks. This program allows the user to alter the window size, dependent on the types of questions being asked. A benefit of using a shifting-window is the ability to see patterns and variation that may not be visible in larger window size comparisons. To test the effects of our ecological and social variables on core unit social networks, we created 20 time-aggregated networks using a 31-day window size and 31-day window shift that spanned the full dataset (August 28th, 2017 to May 13th, 2019). Within

each time-window, a new network was created. To justify our choice of window size, the netTS package tutorials provide guidance on choosing a lower time scale for window-size using a bootstrap technique (Fig. S1). This technique measures the similarity between the observed network in a window and networks created using bootstrap samples from within the window. The idea here is that the similarity between bootstrapped networks and the observed network provides information about the similarity of the observed to the full network (i.e., if perfect sampling was possible), equivalent to the traditional bootstrapping approach (Efron, 1992). To choose a window size above the minimum threshold, we estimated the variability in network density, as window sizes too large will reach asymptote (i.e., density of 1) and window sizes too small will have densities close to 0, resulting in lower variation (Caceres, Berger-Wolf, & Grossman, 2011). The optimal window size, in terms of maximizing variability in edge density, for our data was 31 days. We thus used the netTS package with a window size of 31 days to calculate and analyze social network metrics to determine the connectedness of core units over time. At the node (core-unit) level, we calculated degree (i.e., the number of core units associated with) and strength (i.e., sum of all edge weights for a given node, indicating the total association rate for a given core unit). At the network level, we calculated edge density (i.e., the ratio of the number of edges and the number of possible edges), clustering coefficient (i.e., number of core units associated with that also associated with one another), and cosine similarity (see below). At the dyad level, we calculated dyad association measures (AI).

Statistical Analyses

To analyse the consistency of the core unit social network over time (H1), we used the cosine similarity metric. Cosine similarity is a measure of structural equivalence from 0 to 1 and is equal to the number of common neighbors which two nodes share divided by the geometric mean of their degrees (Newman, 2010). A cosine similarity of 1 indicates that the two nodes have exactly the same ratio and identity of associated units. A cosine of 0 indicates the two nodes do not have any shared associations (Newman, 2010). For this study, cosine similarity was used to measure the changes in associations from one time window to the next (Bonnell & Vilette, 2019). We compared cosine similarity for each core unit to the previous time window to reveal short-term variability, as well as between each window and the first time window in the data set to reveal any long-term variability that may be present.

To examine the effects of ecological conditions on group clustering and the overall connectedness of core units, we modeled how changes in fruit and young leaf abundance and rainfall influenced both node and network level measurements. For network-level measures (i.e., band level) we used linear regression with AR1 autocorrelated errors, while for node-level measures (i.e., core unit) we used a multi-level model with AR1 autocorrelated errors and core-unit identity as random effects, since nodes are repeatedly measured over time. We standardized all independent variables and calculated r-squared (R^2) values to provide estimates of effect size for each model (Gelman, Goodrich, Gabry, & Vehtari, 2019).

To investigate the association between male dispersals and association patterns, we first determined whether there was temporal variability in male dispersal events. We examined the relationship between our ecological variables and the number of males transferring between core units in a given month using a Spearman rank correlation, applying a Bonferroni correction for multiple comparisons ($\alpha = 0.017$). We calculated Monte-Carlo approximated p-values as these are more robust when there are ties in the data (Hájek, Šidák, & Sen, 1999). We then tested whether two core units were more likely to continue to associate after a male transferred between them than would be expected, for up to three months following the dispersal event. Here, we calculated simple association measures (AI) between the dyads with male transfers for three months following the male dispersal event. As a control, we also calculated association indices between each of the core units involved in the dispersal event, and the core units they had each been associated with during the month the male transferred. We used one-sample Wilcoxon signed-ranks tests to determine if the association index between the two core units involved in male transfers was higher than their association indices with control dyads.

All analyses were done using either SOCPROG v.2.9 (Whitehead, 2009) and R v.3.6 (R Core Team, 2019). R packages used includes: netTS (Bonnell & Vilette, 2019); BRMS (Bürkner, 2017), igraph (Csardi & Nepusz,

5

2006), and coin (Hothorn, Hornik, van de Wiel, & Zeileis, 2006).

Results

A Highly Dynamic Network

Throughout the study, core unit compositions remained relatively stable with a total of nine males and one female dispersing between units within the band over the 21-month study period in six dispersal events (i.e., two dispersal events involved the parallel transfer of males). Core unit associations varied over time, and clan composition changed from sample period one to two. Hierarchical cluster analysis showed that, compared to period one, two clans were still evident in period two but one core unit (Newtonia) had switched association between clans. In addition, the formation of the AMU, led to this unit forming its own branch in loose association with the two main clans (Fig. 1). The results of the permutation tests for preferred relationships between core units showed significance for sample period one, and not for sample period two (Sample period one: $CV_{Obs} = 0.484$, $CV_{Rand} = 0.44$, $p = 0.014$; Sample period two: $CV_{Obs} = 0.150$, $CV_{Rand} = 0.150$, $p = 0.8487$). This suggests that core units demonstrated less preference when associating with other units in sample period two. Nonetheless, network metrics between sample period one and two were largely similar with little change in the averages for affinity, strength, centrality (Table S1). Most notably, we saw a decrease in the clustering of units between the two years (sample period 1: CC = 0.48, sample period 2: CC = 0.31).
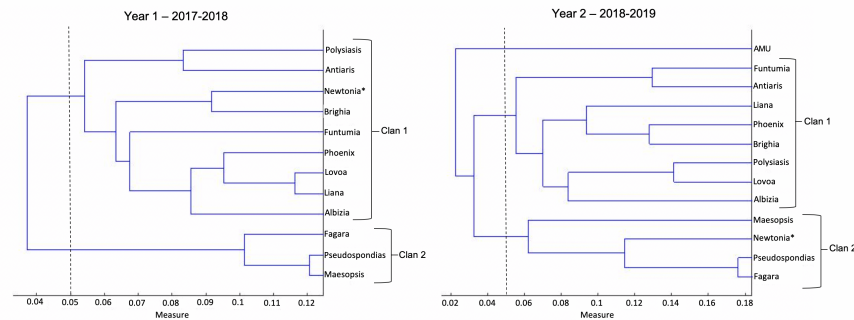

Figure 1 . Comparison of *Colobus angolensis ruwenzorii* core units' clan associations across years at Nabugabo, Uganda, depicted by dendrograms created using hierarchical cluster analysis (CCC = 0.891; SOCPROG: Whitehead, 2009). * indicates the movement of a core unit between clans. The "Year 1 – 2017-2018" dendrogram has been adapted from Fig.1a in Stead & Teichroeb, 2019.

When looking at shorter sample windows, cosine similarity values demonstrate the high amounts of temporal variability within the combined sample years (2017-2019), both in the short-term (Fig. 2a) and the long-term (Fig. 2b). When comparing each window to the first (Fig. 2b), cosine similarity ranges between ˜0.12-0.51 (excluding the first month where cs = 1.0). The highest value of 0.51 was seen in the months of October and December 2017, and the lowest of 0.12 in April 2018. When comparing each window to the previous (Fig. 2a), cosine similarity ranges between ˜0.15-0.61. The highest value of 0.61 was seen in the month of April 2019, and the lowest of 0.15 in November 2018.
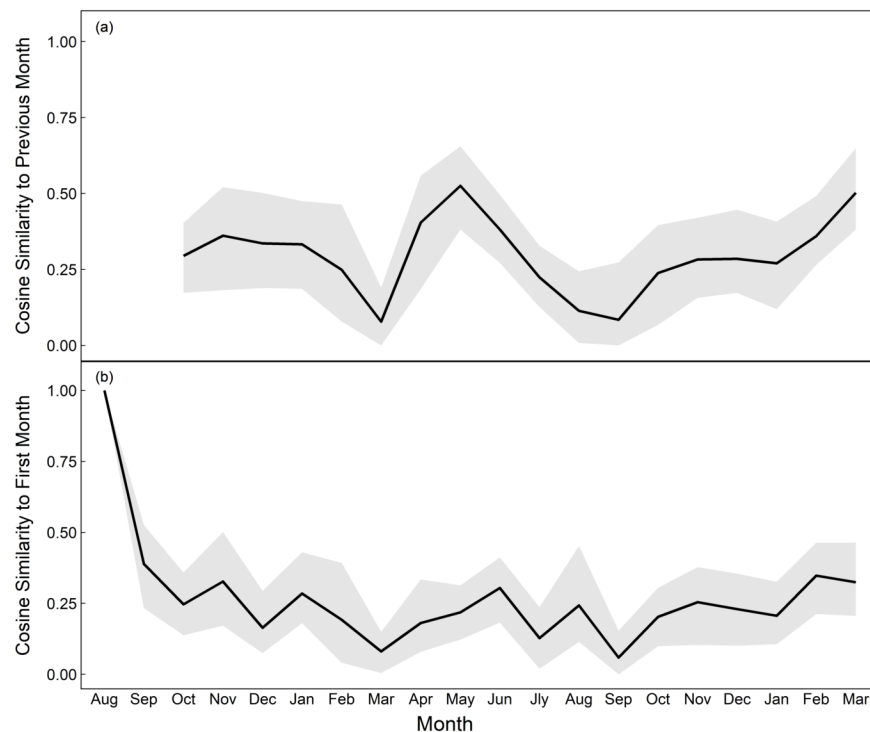
Figure 2. Stability of the social network between core units of *Colobus angolensis ruwenzorii* at Nabugabo, Uganda from Aug. 2017 to May 2019 in both the (a) short-term and (b) long-term, as illustrated by the cosine similarity (a) to the previous month and (b) to the first month of the study period. Shaded areas indicate the 95% highest density interval from 100 bootstrap samples of the observed data.

Ecological Conditions and Association Patterns

Neither rainfall, nor young leaf availability were strongly associated network measures, either at the network level or the node level (Tables 1 & 2; Fig. 3). However, association patterns did correlate with fruit availability. At the network level, fruit availability was weakly but positively associated with both network density and clustering coefficient (Table 1; Fig. 3). At the node-level, fruit availability showed a strong positive relationship with both strength and degree (Table 2); Fig. 3). Thus, core units are more likely to associate with one another, and to form larger aggregations when fruits are abundant, but decrease associations when fruit is scarce (Fig. 3a).

Table 1. Impact that ecological variables (i.e., food availability and rainfall) had on social network measures (i.e., density and clustering coefficient) of *Colobus angolensis ruwenzorii* core units at Nabugabo, Uganda at the network level from Aug. 2017 to May 2019. Note that in the model, all ecological variables were scaled.

	Estimate	Error	Lower 95% CI	Upper 95% C
Density	**Density**	**Density**	**Density**	**Density**
Intercept	0.54	0.06	0.44	0.65
Fruit availability	0.08	0.04	0.00	0.15
Young leaf availability	-0.02	0.03	-0.08	0.03
Rainfall	-0.02	0.03	-0.09	0.05
Clustering coefficient	**Clustering coefficient**	**Clustering coefficient**	**Clustering coefficient**	**Clustering coe**
Intercept	0.63	0.04	0.54	0.72
Fruit availability	0.07	0.03	0.01	0.14

7

	Estimate	Error	Lower 95% CI	Upper 95% C
Young leaf availability	0.00	0.03	-0.06	0.04
Rainfall	-0.03	0.03	-0.08	0.03

Variance explained by models: footnote: density R2 = 0.27 (0.04, 0.49), clustering coefficient R2 = 0.28 (0.05, 0.50)

Table 2. Impact that ecological variables (i.e., food availability and rainfall) had on social network measures (i.e., strength and degree) of *Colobus angolensis ruwenzorii* core-units at Nabugabo, Uganda at the node level from Aug. 2017 to May 2019. Note that in the model, all ecological variables were scaled.

	Estimate	Error	Lower 95% CI	Upper 95% CI
Strength	**Strength**	**Strength**	**Strength**	**Strength**
Intercept	15.95	1.04	13.90	17.89
Fruit availability	2.23	0.68	0.81	3.49
Young leaf availability	-0.89	0.46	-1.78	0.02
Rainfall	-0.85	0.56	-1.89	0.31
Degree	**Degree**	**Degree**	**Degree**	**Degree**
Intercept	5.93	0.24	5.49	6.41
Fruit availability	0.94	0.17	0.49	1.18
Young leaf availability	-0.23	0.14	-0.50	0.05
Rainfall	-0.23	0.16	-0.55	0.09

Variance explained by model's footnote: strength R2 = 0.08 (0.04, 0.15), degree R2 = 0.14 (0.07, 0.22)

Male Dispersal and Association Patterns

There was a significant correlation between the availability of fruits and the number of males transferring between core units in a given month (Spearman: $Rho = 0.50$, $Z = 2.33$, Monte-Carlo approximated p -value = 0.048). Conversely, there was no relationship between the number of male transfers and rainfall ($Rho = 0.14$, $Z = 0.71$, $P = 1.00$), or the availability of young leaves ($Rho= 0.22$, $Z = 1.05$, $P = 0.87$). Thus, male transfers were most likely to occur when fruits were abundant and core units aggregated. Furthermore, the core units in which males transferred between were more likely to keep associating (i.e., maintaining a high AI) than would be expected given their baseline level of association with other units. Analyses revealed significantly higher associations ($P < 0.05$) of the dispersal dyad for 1-2 months post-dispersal than would be expected given their association with control core units (Fig. 4). However, we found that by the third post-dispersal month, all dispersal dyad AIs were no longer significantly different from the null. It is noteworthy that the core unit that switched its clan association from clan 1 to clan 2 between the two sampling periods (Newtonia) may have had this increase in association with clan 2 because five males dispersed from this core unit to a unit in clan 2 (Fagara).
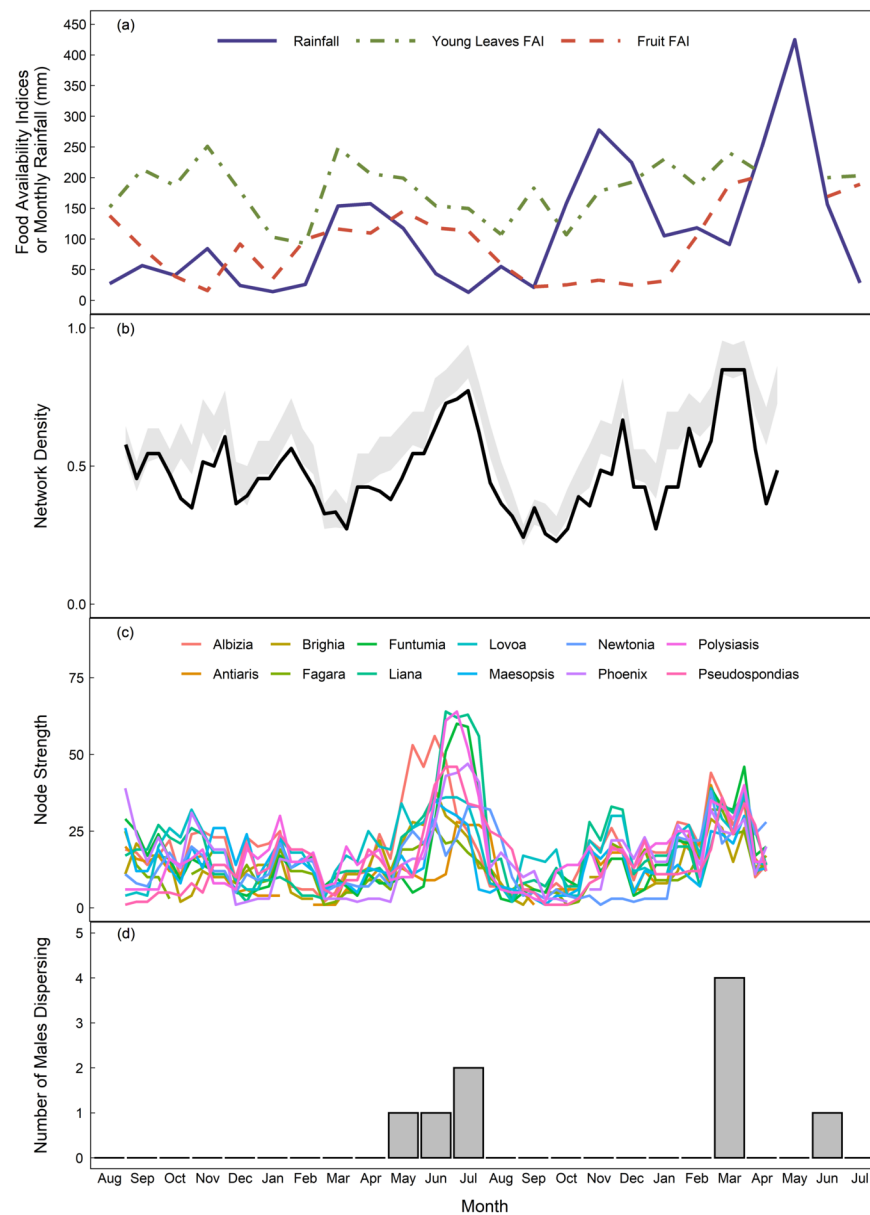
Figure 3. (a) Ecological conditions (rainfall, young leaf and fruit availability) from Aug. 2017 to May 2019 with, (b) social network density measures, (c) node strength, and (d) the timing of male dispersal events in a band of *Colobus angolensis ruwenzorii* at Nabugabo, Uganda. Core unit associations levels are represented by (b) and (c). For (b) the shaded area represents the density range expected due to chance encounters, and was calculated using data-stream permutations using 95% CI.
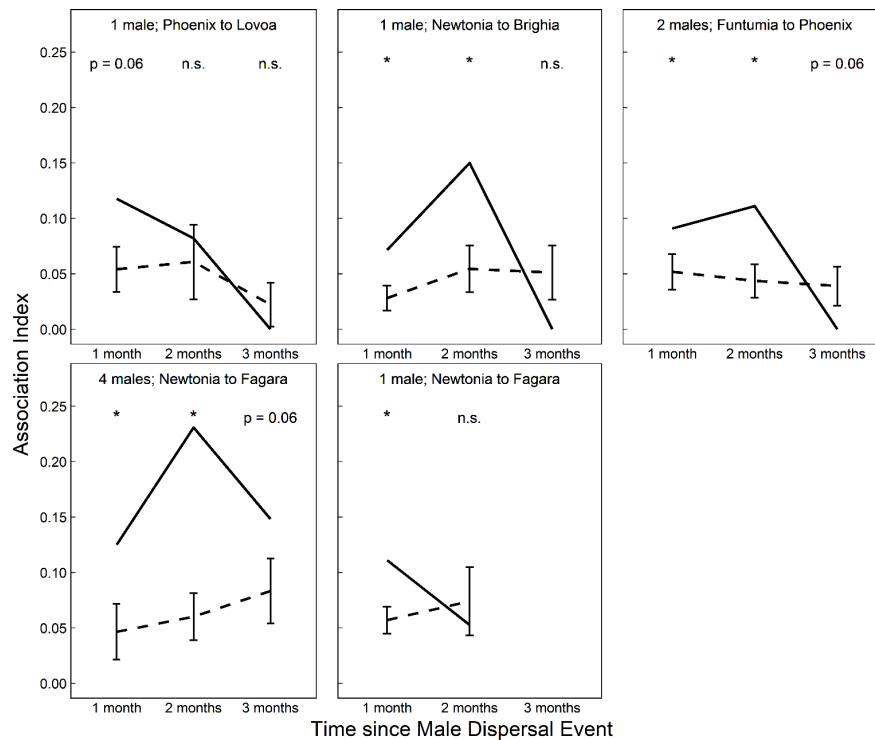
Figure 4. Association indices for the *Colobus angolensis ruwenzorii* core units at Nabugabo, Uganda that males transferred between (solid lines) for the 3 months following each male dispersal event from Aug. 2017 to May 2019. Dashed lines represent expected levels of association, given how much these core units (i.e. those involved in male transfers) continued to associate with other core units not involved in the male dispersal event. (*) indicates association indices that were significantly higher in the core units with male transfer than would be expected at α= 0.05.

Discussion

Our analyses revealed a highly dynamic social network between core units in the *C. a. ruwenzorii* multi-level society. Contrary to our first prediction, the clan tier of organization was not entirely stable over time. Given the importance of kinship in structuring primate groups (Silk, 2001; 2002), we predicted that this may extend to the clan tier of organization, with core units containing related individuals preferentially clustering (e.g., *Papio hamadryas, Theropithecus gelada* , Colmenares, 2004; *Loxodonta africana* , Wittemyer et al., 2005), leading to stable clans within the band. However, we observed two major changes in our study band. First, an all-male unit formed when seven males left the largest core unit and began to range in loose association with the two clans. Second, one core unit moved between clans after dispersal events involving five males. These changes show that clans do shift in core unit composition over time, though not frequently, and that male dispersals can cause this variation.

We found support for our overall hypothesis as both ecological and social variables were important in determining the amount of association among core units. Association patterns fluctuated at both the node and network level, with the largest changes correlating to seasonal shifts in fruit availability. As predicted, core units were more likely to associate, and did so with a larger number of other core units, when fruits were abundant, suggesting that food competition limits operational group size when fruits are scarce. This increase in association appeared to facilitate male dispersals between core units in the band, thus creating a seasonal dispersal pattern. Our analysis of association indices following each male dispersal event within the band revealed that male transfers promote higher than expected dyadic associations between interacting

10

core units in the short-term (1-2 months post-dispersal).

Many species alter their behaviour in response to changing climatic and resource conditions (Candolin & Wong, 2012). Our results show that *C. a. ruwenzorii* is no exception. Similar to studies done on other primates (*Cercocebus torquatus,* Dolado, Cooke, & Beltran, 2016; *Rhinopithecus bieti,* Ren, Li, Garber, & Li, 2012; *Papio hamadryas*, Schreier & Swedell, 2012b; *Pongo pygmaeus,* Sugardjito, Te Boekhorst, & van Hooff, 1987) and non-primates (*Orcinus orca,* Foster et al., 2012; *Loxodonta africana* , Wittemyer *et al.,* 2005), we found that *C. a. ruwenzorii* units increase their association levels during times of peak food availability. Food competition decreases when resources are abundant, allowing animals to aggregate if they choose, which provides benefits for predator avoidance (Hamilton, 1971; Sueur et al., 2011). Species living in a multi-level society benefit from this ability to alter overall group size in response to external pressures (Grueter & van Schaik, 2009). For *C. a. ruwenzorii* , enlarged group size may even mean an expansion of the microhabitats they are willing to take advantage of. Adams and Teichroeb (2020) found that at Nabugabo, where predation risk is greatest near the ground, *C. a. ruwenzorii* were willing to come lower in the canopy to find food when more core units were clustered together and predation risk was lessened. The analyses presented here suggest that this niche expansion may occur more often in resource rich seasons when core units are able aggregate.

Although we find correlations between seasonal fruit availability, association patterns and male dispersal, it is important to acknowledge that we cannot determine cause and effect between these phenomena. While we posit that higher fruit availability leads to more clustering among core units, which facilitates male dispersal, it is possible that males prospect more during seasons of food abundance and that male prospecting behaviour drives the observed changes in association patterns. Seasonal dispersal patterns are found in many species (Likicker & Stenseth, 1992) but in most cases, this pattern emerges due to seasonal breeding (e.g., *Presbytis entellus,* Borries, 2000; *Suricata suricatta* , Mares et al., 2014; *Chlorocebus pygerythrus,* Young et al., 2019; *Rhinopithecus roxellana,* Yao et al., 2011). Breeding is not typically seasonal in black-and-white colobus monkeys (Fashing, 2011) and we do not have data showing seasonal breeding at Nabugabo. Alternatively, it is sometimes advantageous for animals to time dispersal to coincide with high food availability because it allows them to compensate for increased travel, potentially in unfamiliar areas (Pusey & Packer, 1987; Isbell & Van Vuren, 1996). This explanation is unlikely to apply in a multi-level society like that seen in *C. a. ruwenzorii* as all the core units in our band share a home range (Stead & Teichroeb, 2019). Consequently, male dispersal between units does not require extra travel or moving into a new, unfamiliar area. We suggest that the best explanation for the seasonal pattern of male dispersal that we observe in *C. a. ruwenzorii* is the opportunity for prospecting provided by greater core unit clustering due to high resource availability. The proximity of so many other core units allows males to assess their composition (i.e., sex ratio) as well as the competitive ability of the males there (Teichroeb et al., 2020), potentially influencing their decision to disperse. In primates, it is common for dispersal to occur during intergroup encounters (e.g., *Macaca mulatta* , Boelkins & Wilson, 1972; *Erythrocebus patas* , Rogers & Chism, 2009; *Gorilla beringei* , Sicotte, 1993; *Rhinopithecus roxellana* , Yao et al., 2011) or to groups where prospecting has previously been directed (e.g., *Colobus vellerosus* , Teichroeb, Wikberg, & Sicotte, 2011).

The persistence of high association indices post-dispersal for core units that have males transfer between them may be a result of the continued bonds between individuals that persist even after the dispersal has taken place. The dispersing individual(s) likely still have ties in their former (sometimes natal) unit, which may contain many kin. However, over time, we see a slow decrease of association between the units individual(s) dispersed to and from, back to the baseline association levels that they had prior to the dispersal event. This decrease in association may be explained by the further integration of the dispersing individual(s) into their new unit, and/or the seasonal decrease in fruit availability, and subsequent increase in food competition. Future research examining how male-male genetic and social relationships impact association patterns over short and long time periods will provide insights into the ways that kinship structures core unit association in tandem with ecological and social factors (e.g., Snyder-Mackler et al., 2014).

To conclude, our results show that in the dynamic social network of Rwenzori Angolan colobus monkeys, core

units behaviourally adapt to changing ecological conditions by altering their association patterns. Doing so has cascading effects on the composition of core units, and structure of both the clan and band tiers in this multi-level society. This type of behavioural flexibility allows animals to thrive in dynamic environments (Candolin & Wong, 2012). Our study provides a deeper understanding of the mechanisms underlying the formation of complex multi-level social organizations and some insight into the intertwined temporal effects of ecological and social variables.

Author contributions

FVA and JAT conceived the study. JAT provided funding. JAT and SMS organized data collection. All authors contributed to data analysis and writing the manuscript.

Data availability

Upon acceptance of this manuscript, data will be made available as supplementary material.

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