SOCIALITY AND THE MICROBIOME: GUT MICROBIAL CONVERGENCE WITH INFANT PRESENCE IN THE BLACK-AND-WHITE COLOBUS MONKEY (*COLOBUS VELLEROSUS*)

by

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While recent studies in wild primate populations have demonstrated that social behavior plays an important role in gut microbial variation, there is limited understanding of how changes in social cohesion affect the composition of the gut microbiome. This study provides a more comprehensive examination of this longitudinal relationship in a natural population of black-and-white colobus monkey (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana. Adult female *C. vellerosus* display an overall increase in social interaction after the birth of an infant, presenting a known social shift that I utilized in conjunction with gut microbial samples to explore the association between increased social cohesion and the composition of the gut microbiome. I used previously collected field data (2018-2020) from all adult females across four social groups of *C. vellerosus*, resulting in 218 total fecal samples and a mean of 17.2 focal hours of behavioral data per female (SD +/- 3.96). I used these data to characterize microbiomes using 16S rRNA sequencing and quantify changes in social cohesion in the presence of an infant. I found that the presence of an infant was significantly associated with a change in gut microbial similarity across all groups (PERMANOVA: $p<0.01$), and for three of the four social groups, adult female gut microbiomes become more similar after an infant is born (GLMM: $p<0.036$). However, social network analysis did not reveal significant changes in social cohesion with a young infant present, indicating that other changes in social interactions not included in my analyses may help explain this pattern. Based on these findings, future work would aim to evaluate the basis for differences in gut microbial variation between social groups and explore

the presence of allocare and grooming rates in this study population with a young infant present. Investigating the relationship between changes in social interactions and the mechanisms of microbial variation ultimately contributes to our understanding of the factors influencing the assembly, composition, and diversity of the gut microbiome.

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Introduction

The Gut Microbiome and the Host

The gut microbiome consists of the community of microbes inhabiting the gastrointestinal tract of a host organism. In vertebrates, while the gut is initially colonized at birth and perhaps in utero, the microbiome exhibits considerable compositional variation throughout an individual's lifetime. These fluctuations have been found to have a range of implications on host physiological development and function. Gut microbial composition has been shown to be essential for nutrient uptake and prevention of pathogenic invasion (Suzuki et al., 2017), immune system development (Hooper et al., 2012), and development and function of the brain and associated behavior via the gut brain axis (Jena et al., 2020). Imbalances in the gut microbiome, known as dysbiosis, may lead to disruptions in these processes and cause consequences for the host. For example, studies have found evidence of associations between dysbiosis and obesity (Amabebe et al., 2020), depression (Kelly et al., 2016; Radjabzadeh et al., 2022), anxiety (Clapp et al., 2017) autism-like symptoms (Hsiao et al., 2013), and diabetes (Li et al., 2020). The extensive consequences of dysbiosis have caused the gut microbiome to gain considerable attention in clinical research as a system which has important implications for human health. Work in this area seeks to develop methods which could utilize gut microbes for medical applications concerning preemptive and ad hoc therapeutics for disorders correlated with dysbiosis. While our understanding of the relationship between host function and the gut microbiome continues to advance, we still lack a basic understanding of what factors act to shape the host microbiome and cause natural variation.

Social Factors Shaping the Gut Microbiome

Past work has described factors at both the host and environmental level which have been shown to have some influence on gut microbiome variation including host diet, genetics, and social environment (Archie & Theis, 2011). The influences of host diet and genetics on gut microbial composition have been studied extensively, however less work has been done to investigate the aspects of the host social environment which influence the gut microbiome. As clinical intervention continues to exist at the forefront of microbiome research, understanding these social factors that contribute to microbial variation has valuable implications for the host which could ultimately inform on approaches to shape a healthier gut microbiome. Exploring social transmission of gut microbes may also help explain the evolution of sociality as the sharing of microbes has been found to confer benefits for group members such as increased pathogen resistance and host immunity (Abt & Pamer, 2014; Ezenwa et al., 2016; Koch & Schmid-Hempel, 2011; Lombardo, 2008).

Some evidence of microbial transmission through social mechanisms has been explored in human subjects; studies have found cases of socially mediated microbial transmission through evaluations of cohabitation in adulthood (Gacesa et al., 2022; Lax et al., 2014; Song et al., 2013; Valles-Colomer et al., 2023) and infant adoption (Tavalire et al., 2021). While human studies provide valuable evidence of socially mediated microbial transmission, detailed characterization of human social behavior can be difficult. Non-human primates provide an ideal alternative study system for questions related to sociality and the gut microbiome due to their highly studied nature, the ability to collect detailed behavioral, dietary, and relatedness data, and their behavioral and phylogenetic similarities to humans. Studies in this area have worked to isolate

and evaluate the relationship between host social environment and the non-human primate gut microbial composition.

In one of the earlier papers on this subject, Tung et al. (2015) evaluated the importance of social group membership and social networks on the structuring of the gut microbiome in a wild population of baboons. Excluding kinship, shared diet, and shared environment in their evaluation, the study found social grooming networks to be predictive of gut microbial similarity; rates of interaction between individuals directly related to compositional variation in the gut microbiome. Other studies have found similar evidence of socially mediated gut microbial transmission in this population of baboons (Grieneisen et al., 2017) as well as other non-human primate species including Verreaux's sifaka (Perofsky et al., 2017), black howler monkeys (Amato et al., 2017), and ring-tailed lemurs (Bennett et al., 2016).

While these studies provide a better understanding of the social factors that serve as mechanisms for microbial transmission at a cross-section in time, the rapidly changing nature of the gut microbiome implores future work in this area to focus on more comprehensive longitudinal surveys with daily to weekly sampling of individuals spanning multiple years (Björk et al., 2019). There are a number of recent studies which have taken this approach in non-human primates and have begun to disentangle the factors which may contribute to inter- and intra-individual gut microbial variation. Analyses of well documented populations of chimpanzees over eight years (Moeller et al., 2016) and wild baboons over 13 years (Ren et al., 2016) revealed microbial variation correlating with both host-specific and environmental factors. In Verreaux's sifaka, environmental factors were found to define the population level gut microbial signature while patterns of host social interactions facilitated the persistence and variation of gut microbial communities over time within groups (Perofsky et al., 2021; Rudolph et al., 2022). In red-bellied

lemurs, patterns of social contact (group membership and position within the social network) predicted gut microbial composition (Raulo et al., 2018), and distinct gut microbial signatures were detected in two daughter groups of black-and-white colobus monkeys less than nine months after a fission event (Goodfellow et al., 2019). This research project aims to add to this growing body of work using a combination of fine-grained data on primate social behavior and deep longitudinal sampling of individual gut microbial compositions within social groups.

With a longitudinal approach in mind, I was specifically interested in evaluating how changes in social cohesion influence gut microbial variation. In the context of my project, social cohesion refers to the average physical proximities between members of a social group. To my knowledge, there is only one paper that has directly evaluated this mechanism. The 2019 study looked at human cohabitation and closeness in relationships with siblings and married couples as their study subjects. As in previous studies, they found that individuals cohabitating with a spouse or partner had more similar gut microbiomes than unmarried, non-cohabitating individuals. Most importantly for the purposes of my project, the authors found that that spouses and siblings that rated themselves as having relatively "close" relationships had more similar gut microbiomes than pairs which did not rate themselves as having "close" relationships (Dill-McFarland et al., 2019). My research builds on these results by tracking expected changes in social cohesion gut microbial variation over time in a well-documented non-human primate population.

Research Objectives and Hypotheses

Colobus vellerosus and Allomothering: a model for social shifts

To explore my research question, I focused on a population of black-and-white colobus monkeys (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana. The population of colobus monkeys at this site has been studied since 2000, leading to a detailed record of their behavior and group compositions. There are approximately 28 social groups in the area composed of uni- or multi- male/multi-female social groups with sizes ranging from 9-38 individuals (Kankam & Sicotte, 2013; Wong & Sicotte, 2006). Recent work on the BFMS black-and-white colobus population compared diet, relatedness, and the 1 m proximity network to see which factor was the best predictor of differences in the gut microbiome across eight social groups. The study found that models of social connectedness in the 1 m proximity network best predicted variation in the gut microbiome composition between individuals (Wikberg et al., 2020). As in other non-human primate species, these results support the concept of social interaction as a factor mediating gut microbial transmission. The study also showed that microbial transmission can occur in species with low rates of social interaction (grooming, time in close proximity) relative to other gregarious primate species (Teichroeb et al., 2003) and that proximity networks can be sufficient for predicting microbial transmission.

The subfamily of monkeys to which black-and-white colobus belong (subfamily Colobinae; or colobine monkeys) are known to exhibit relatively high levels of allomothering behavior, described as an individual's attraction to and handling of another's infant (Bădescu et al., 2015; McKenna, 1979). In order to gain access to a young infant, females will spend increased amounts of time grooming the mother, and thus overall grooming rates increase and individuals spend more time in close proximity when an infant younger than 3 months old is

present in a group (Wikberg et al., 2015). Thus, based on previous research that showed 1) social interactions affect gut microbial variation and 2) social interactions change in the presence of an infant, I used black-and-white colobus monkeys as a model to evaluate the following question and hypotheses:

QUESTION: How is gut microbial similarity influenced by the presence of infants within social groups of adult female black-and-white colobus monkeys?

Objective 1: Compare gut microbial similarities of adult females during time periods with and without a young infant present.

> **Hypothesis 1:** Female group members will have more similar gut microbiome compositions when a young infant is present in their social group than they will in the absence of a young infant.

Objective 2: Evaluate changes in social cohesion during time periods with and without a young infant present.

> **Hypothesis 2:** Adult female group members will display higher levels of social cohesion when a young infant is present in a social group than they will in the absence of a young infant.

I used detailed demographic, behavioral, and microbial sampling from four social groups of black-and-white colobus monkeys at BFMS to quantify the longitudinal relationship between social environment and gut microbial variation. I first tested whether periods with and without

young infants present correlated with variation in the gut microbial compositions of adult females in each social group. I then evaluated the type of variation that was occurring; if it was in line with my hypothesis, I expected to see adult female gut microbiomes becoming more similar to each other when a young infant was present. Next, I used social network analysis based on 1 m proximity networks to evaluate changes in social cohesion with a young infant present. My goal was to test if the presence of an infant led to changes in gut microbiome similarity across the social groups, and then to see if changes in social cohesion (proximity) based on allocare behavior could be a factor contributing to this microbial variation. This research is novel and significant because it utilizes a longitudinal approach to known social shifts surrounding infant care and employs a fine-grained data set with well-coupled behavioral and microbial sample components. The results of this study expand our understanding of the effects of changes in the social environment on the compositional variation of the gut microbiome on defined temporal scales.

Methods

Part 1: Fieldwork and Labwork

University of Oregon graduate student Diana Christie conducted the fieldwork and labwork portions of this research. This included behavioral data collection and fecal sample collection from the study population (*Colobus vellerosus;* Boabeng-Fiema Monkey Sanctuary; Ghana). These methods have been described elsewhere (e.g., Goodfellow et al. 2019; Wikberg et al. 2020), but they are briefly documented here to provide context for the downstream data processing and analyses that I conducted.

Christie and her field assistants focused on four social groups for behavioral data collection (Redtail/RT, Wawa/WW, Winter/WT, and Splinter/SP), each containing habituated and identified individuals. Behavioral data were collected from all adult females within the four groups between 2018 and 2020, yielding two consecutive dry seasons of data. Samples were collected in the dry season (~December to April) to avoid the effects of seasonal variability on gut microbial composition (Gomez et al., 2015; Springer et al., 2017). Behavioral data were collected via continuous focal sampling, which involves tracking one individual at a time and recording frequency, duration, and type of behavior exhibited by the focal subject. This method was used to record behaviors during 10-minute intervals for all adult females in each social group (see Supplementary Figure 1 for a full list of behaviors). Social and feeding behaviors were recorded continuously. During a focal, point samples were also taken every 2.5 minutes identifying all individuals within 0, 1, 3, and 5 meters of the focal subject. Behavioral data collection yielded a total of 240.84 hours of focal samples (mean 17.2 hours per female SD +/- 3.96).

Christie and her field assistants collected fecal samples during the same periods of time they were collecting behavioral data. Multiple samples were systematically collected from each focal subject to be used for gut microbial composition characterization via 16S rRNA sequencing. Fecal samples were collected monthly for adult females. After an identified individual defecated, 1-2 g of feces were collected using gloves and sterile collection sticks and dissolved in 4 ml of RNAlater®. The samples were stored in a freezer on site before being shipped to the Ting Lab at University of Oregon for storage at –20 °C. For the purposes of this study, these samples were used to represent the gut microbiome, however it is understood that there may be differences between the microbial composition of the samples and the true microbial communities of the host gut microbiome. Therefore, although it is more accurate to say that the samples characterized the hindgut or fecal microbiome, they were used in this context to evaluate socially mediated transmission of gut microbes between individuals.

Christie extracted DNA from each fecal sample using the Qiagen PowerFecal Pro kit, and DNA extracts were quantified on a Qubit Fluorometer. The V4 hypervariable region of the 16S rRNA gene was targeted for sequencing as this region is useful for identifying taxa at the level of genus or species (Bukin et al., 2019). Library preparation followed protocols described in Goodfellow et al. (2019), and sequencing was conducted on a 300 base pair paired-end run on the Illumina MiSeq platform. Demultiplexing was completed by the core, matching each sample name with its appropriate set of sequenced rRNA reads. These steps produced fastq format files for each sample containing all reads for that specific sample.

Part 2: Data processing

Behavioral data

The raw behavioral data were encoded in CSV files. I processed these using a combination of Microsoft Excel, Microsoft Command Prompt (CMD), and R (R Core Team, 2021). I first manually cleaned the data in Excel; any cells that were flagged for missing information were corrected and additional information was added where necessary. I then ran each sheet of focal data through a series of Command Prompt checks which involved ensuring files were in CSV format, removing Excel formatted files, eliminating any spaces in file names or quotation marks in cells, then checking for missed corrections from the manual cleaning. Any missed corrections were subsequently fixed again in Excel, and the processing steps above were repeated. Incorrect ethogram codes were also located using an R script which would return a file with problem focal sheets. These codes were corrected and the script was rerun to ensure all inaccuracies were accounted for before the data were formatted for use in R. The overall results of the behavioral data processing included monthly pairwise social matrices for all adult females, and presence/absence of infant under 3 months. If infants were present, the number of infants under 3 months was also included.

Sequence data

Data processing of 16S sequence reads was carried out on the University of Oregon's high performance computing cluster, Talapas, using the bioinformatics processing pipeline QIIME2 (Bolyen et al., 2019). I began by creating a bash script which would allow me to run slurm jobs as I worked through the pipeline. I used the DADA2 (Callahan et al., 2016) plugin for the next series of steps in processing. As each sample was read in both the forward and reverse direction during sequencing, I chose parameters to allow for the appropriate level of overlap

between the reads before they were realigned, a process known as denoising. Too much overlap causes the program to throw out more reads as it detects a higher number of unmatched bases, but too little overlap runs the risk of incorrect matches between reads. The values I ended up choosing were determined using a combination of quality score plots generated in the demultiplexing summary and trial and error. My parameters specified a total length of 274 base pairs (~20 base pair overlap), resulting in an average of 88.3% of reads successfully merged per sample (see Supplementary Figure 2 for denoising summary statistics). Once the sequences were aligned, the final step in processing was choosing appropriate sampling depth parameters, a process that results in the removal of samples with relatively low numbers of reads to maintain a robust data set for analysis. I conducted taxonomic classification using the SILVA database (Quast et al., 2013). The outcomes of microbial sample processing included an ASV table, a phylogenetic tree, and taxonomies.

Metadata file creation

Using demographic and sample data, I produced a metadata file in CSV format which contained information related to each fecal sample. This metadata file was used for much of the initial processing and in QIIME2 as well as other downstream analyses. Pertinent metadata information for each sample included collection month, field season, fecal time point (a period of days within a field season where fecal samples were collected for all adult females in a social group), infant presence, and number of infants present. Infant presence was calculated by referring to a demography data sheet which lists all birth and death/disappearance dates for infants in each of the four social groups. Based on work in mice where microbial variation was tracked after cohousing (Caruso et al., 2019), I estimated the length of time for the gut microbiome to show significant levels of compositional change in an individual to be three days

after the birth of an infant with the assumption of social changes immediately after birth. After this window of time was determined, I reviewed the infant presence periods I created and found no instances of samples collected within three days of an infant birth or an infant death/disappearance and thus no samples needed to be removed from my data set. See Supplementary Figure 3 for the full metadata sheet.

Generating a distance matrix

I used the qiime2R package (Bisanz, 2018) to import my data from the QIIME2 pipeline into R. With the features table, phylogenetic tree, and taxonomy table from QIIME2 and the metadata file, I used the phyloseq package to create a phyloseq object, a way for microbial information to be stored, manipulated, and analyzed in R (McMurdie and Holmes, 2013). The data were then filtered to remove any samples with fewer than 5000 reads for quality control, removing 9 samples out of the original 218. As there was a chance some taxa would have only appeared in those samples that were removed, I included a command to remove empty spaces in the taxonomy table. I also included a command to remove sequence reads that mapped to chloroplasts or mitochondria instead of the ASV's I was interested in analyzing as DNA derived from these organelles also contains the 16S gene and can represent a source of contamination.

The next step in preparing the data for statistical analysis was creating a distance matrix of beta diversity indices using Aitchison distance. Beta diversity refers to the compositional dissimilarity between microbial communities. Evaluating levels of similarity between samples allows for the partitioning of how various factors may be influencing compositional similarity of the gut microbiome between individuals. I first centered log-ratio (CLR) transformed the data, converting the values from total counts to the dominance for each taxon relative to the mean of all taxa (Gloor et al., 2017). Next, the distance matrix was generated with these data using the

Euclidean method. These two steps generate an Aitcheson distance matrix. This distance is widely employed for microbiome work as it has been shown to better account for the compositional nature of microbial data and avoid compositionality bias (Quinn et al., 2018). The distance matrix itself gives dyadic measurements of microbial similarity between all individuals in which the numerical measures in this case are based on the Aitchison beta diversity metric.

Part 3: Statistical analysis

Preliminary analysis

Before beginning my analyses, I used a microbiome analytics tutorial to obtain preliminary statistics for my data set and to develop microbiome analysis skills in R using real data. I calculated and plotted the relative abundance of the phyla and observed richness using the phyloseq (McMuride and Holmes, 2013) and ggplot (Wickham, 2016) packages in R. For beta diversity analysis, I generated an Aitchison distance principal coordinate analysis using the packages microbiome (Lahti and Shetty, 2017) and vegan (Oksanen et al., 2022).

PERMANOVA: Testing for the presence of changes in microbial similarity

A permutational multivariate analysis of variance (PERMANOVA) identifies the effects of various factors on microbial variation and their interactions with each other via a permutational ANOVA of a distance matrix (Anderson, 2001). Broadly, the test asks if microbial variability is greater between groups or within groups for a given sample, displaying significance if variability is greater between groups. I ran a specialty version of a PERMANOVA called an adonis using the adonis2 function of the R package vegan. For the purposes of my study, I tested for differences in gut microbial similarity between time periods with and without a young infant present while controlling for other factors shown to have significant effects on gut microbial

variation. While collection year and field season were both included in the metadata sheet, I chose to exclude collection year as a factor as it is similar to field season, and field season better describes temporal changes between collection periods.

In setting up the command, each factor could be incorporated in an additive fashion, or if I wanted to test for interactions between factors, it could be incorporated in a multiplicative fashion with another factor. Preliminary analysis involved running the PERMANOVA with different variations of factor interactions, which revealed significant interactions between social group and infant status, and between field season and collection month. Therefore, the final formula structure I used included a multiplicative interaction between social group and infant status, a multiplicative interaction between field season and collection month, and individual ID as an additive factor to account for repeat sampling among individuals.

Generalized Linear Mixed Model (GLMM): Evaluating changes in distance to centroid

In the second part of my microbial analysis, I specifically wanted to test if changes in beta diversity (microbial similarity) with the presence of an infant were being driven by individuals in a group becoming more similar to one another in gut microbial composition. To do this, I modeled the effect of infant presence on distance to centroid (DTC), which measures how dispersed members of a group are from a central location. Because in this case, dispersion of points correlates with the level of microbial similarity between samples, the measure of distance to centroid can be used to compare microbial similarity between groups (See Figure 1). I used phyloseq to subset the data by fecal time point and create Aitchison distance (beta diversity) matrices, then used the usedist package (Bittinger, 2020) to generate distance to centroid measurements for each fecal time point.

The most appropriate way to handle repeat sampling in my data was to utilize a mixed effects model to account for random effects in addition to fixed effects. A Shapiro test for normality revealed the data were non-normal and thus unfit for a linear mixed effects model. Therefore the glmmTMB package (Brooks et al., 2017) was used to run a generalized linear mixed model (GLMM) as it does not rely on normality as an assumption. To improve the fit of the GLMM, the outcome variable (DTC) was also log transformed. The best factor interactions for the gamma fit test were determined using AIC based model selection (models with lowest AIC values were chosen) and the drop function in R. The selected model structure included the log link model of the GLMM with infant status as a fixed effect and group, ID and collection month as random effects. Field season was excluded as a factor as it could not converge as a fixed or random effect. The model was compared to the null model which fitted the data by only the random effects without infant status. The effects of the model were plotted using the effects package in R (Fox and Weisberg, 2019; Fox, 2003) to visualize the interactions between the DTC and infant status.

Because the social group Winter (WT) showed divergent patterns in the results of the GLMM (see Results), it was eventually removed from the data set, and model selection and drop were used to determine the best factor interactions. Without WT, this was a log link model of the GLMM with infant status as a fixed effect and ID and collection month as additive random effects. This model was also compared to the null model, and the effects of the model were plotted again using the effects package in R.

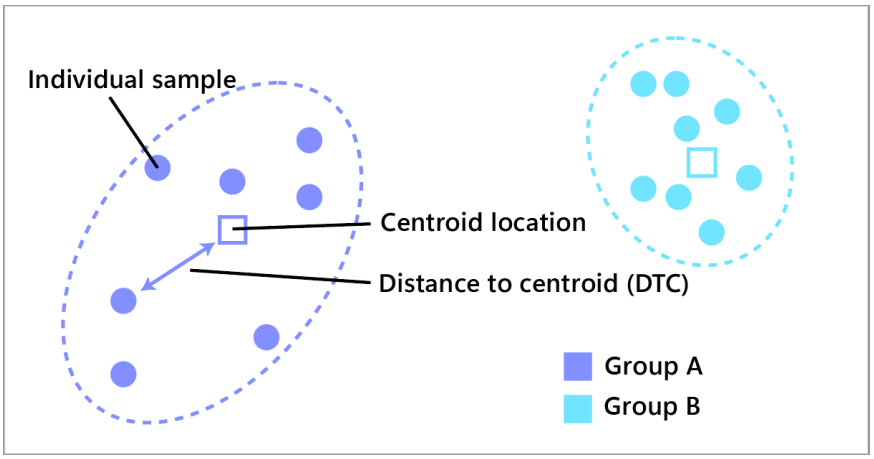


Figure 1: Conceptual Figure of Distance to Centroid. Distance to centroid measures how dispersed all members of a group are in relation to a central point (centroid location). In this case, individual samples refer to the microbial samples, and the distance to centroid was calculated based on Aitchison distance metrics (Quinn et al., 2018).

Social networks and centralization: Evaluating changes in social cohesion

Social cohesion in this study refers to the average level of physical proximities between all adult female members in a social group. Higher social cohesion, for example, would correlate with individuals spending more time in close proximity. In order to explore changes in social cohesion associated with infant presence, I used social network analysis, a method of calculating standardized sociability measures that allows for evaluation of relationships within social groups (de Lima & Ferreira, 2021). This approach generates social networks in which points (nodes) represent individuals and the lines between points (edges) represent the social interactions of those individuals.

For each social group, the time periods where infants were present and absent were determined, and the data were subset by infant status (young infant present = Y or N). This resulted in nine social networks being generated; there were two "Y" and one "N" infant status time periods for each social group. All networks were constructed using continuous approaches

to within 1 meter from the focal follows collected by Christie during field sampling. The social group Redtail (RT) was excluded from this analysis because it did not have a minimum of 1 "Y" and 1 "N" infant status period with sufficiently dense behavioral data. Each distance matrix was loaded into R studio and converted to an undirected weighted edgelist using igraph (Csardi and Nepusz, 2006). Exploratory modularity analysis was run for each matrix using igraph, applying an optimization algorithm which identified groups of strongly connected individuals ("communities") in the network, differentiating each via color overlays on the social networks (Brandes et al., 2008). Igraph was also used to run a statistical analysis of network-level metrics for the centralization of the social groups, which included evaluation of degree, closeness, betweenness, and eigenvector centralization values, each measuring different aspects of social structure within a group. Given the relatively small size and well-connected nature of the social groups, I chose to focus on eigenvector values for my statistical analysis as they consider both number and strength of connections, capturing the greatest amount of variation in my data (Hanneman and Riddle, 2005).

To evaluate the relationship between infant status and the social cohesion (eigenvector centralization) of adult females in a social group, I used a nested ANOVA in R. For my data sheet, I included the eigenvector values in a table along with IDs for each social network (SPY1, SPN1, etc.), social group (SP, WW, WT), and infant status (Y/N). To test for a significant difference in social cohesion with or without a young infant present across all social groups, I ran the nested ANOVA with social group nested within infant status.

I also ran the same set of tests with a different social network metric called mean network strength. While eigenvector centralization describes the extent of cohesion around particular focal individuals in a group, mean strength more generally describes how connected all

individuals are to each other, which is similar to the method used in Wikberg et al. (2015). To calculate this metric, I found the average value for each social network matrix, making sure to have each dyad represented one time. I ran the same nested ANOVA discussed above using this second network metric. I chose to run tests using both types of network metrics because they measure social structure in slightly different ways and significant results for either one would provide insight into how social cohesion might vary with the presence of an infant.

Results

Preliminary analysis

After filtering, there were 209 total samples with an average of 79,254 reads per sample. There were 30 phyla and 3828 taxa represented in the data set. As expected, observed amplicon sequence variants (ASV) were found to correlate with total read count. From a visual overview, the principal coordinate analysis (PCoA) displayed subtle differences in gut microbial clustering and dispersion between the four social groups (Figure 2).

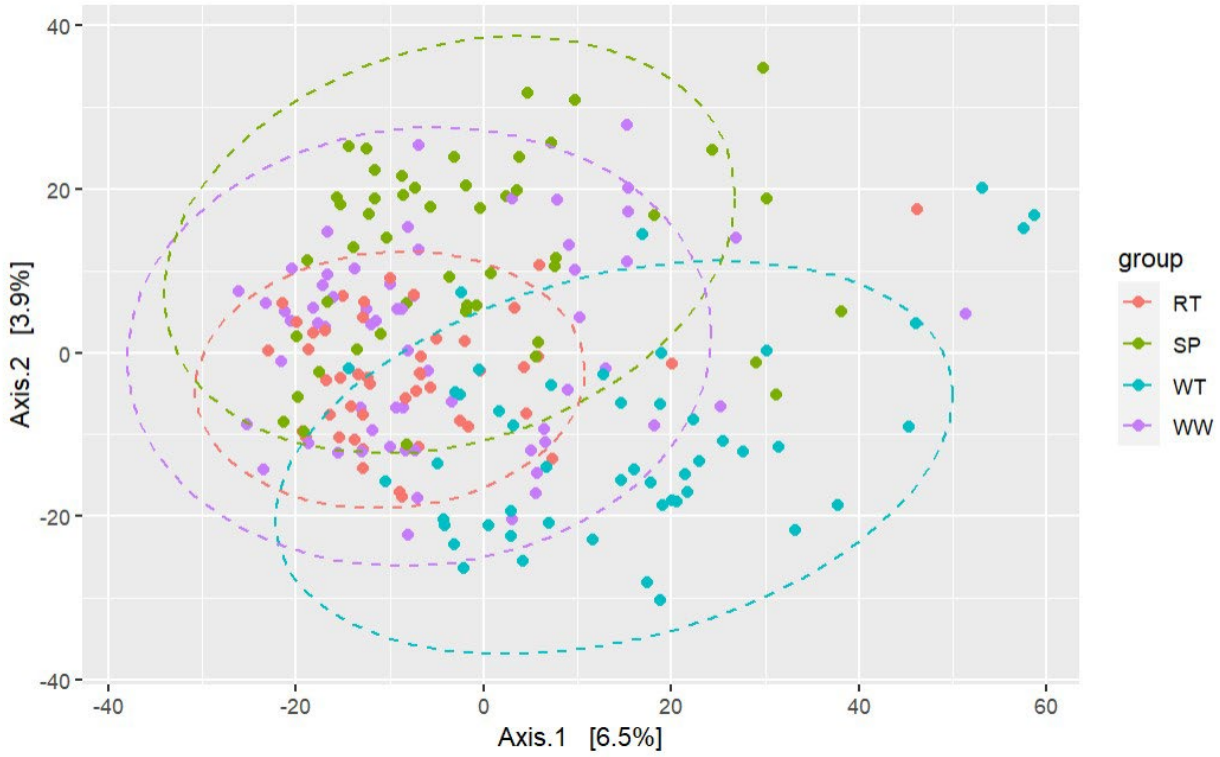


Figure 2: Principal Coordinate Analysis. Ordination plot generated from the identified principal coordinates of my data set. The four social groups displayed differences in clustering and dispersion based on Aitchison distance metrics.

PERMANOVA

All factors of interest showed significant effects on beta diversity (microbial similarity); collection month ($R2=0.04456$, $p<0.001$) and field season ($R2=0.03502$, $p<0.001$) explained a moderate amount of variation in beta diversity and had a significant interaction ($R2=0.01995$, $p<0.001$). After controlling for all other variables, infant presence had a small but significant effect on gut microbial variation ($R2=0.007131$, $p<0.001$). Social group and infant presence also had a significant interaction after controlling for other variables ($R2=0.01907$, $p<0.001$). See Table 1 for a full summary of PERMANOVA results.

	Df	SumOfSqs	R2	F	Pr(>F)
group	3	79437.033	0.0825626	7.688397	0.001
inf.pres	1	6861.465	0.0071314	1.992282	0.001
field.season	4	33692.438	0.0350181	2.445719	0.001
coll.month	7	42871.560	0.0445584	1.778301	0.001
id	22	196921.537	0.2046697	2.598990	0.001
group:inf.pres	3	18344.420	0.0190662	1.775484	0.001
field.season:coll.month	4	19194.826	0.0199501	1.393344	0.001
Residual	164	564819.659	0.5870434	NA	NA
Total	208	962142.938	1.0000000	NA	NA

Table 1: Summary of PERMANOVA Results. All factors of interest showed significant effects on beta diversity. Infant presence exerted a small but significant effect on beta diversity ($R2=0.007131$, $p<0.001$). Social group and infant presence also showed a significant interaction ($R2=0.01907$, $p<0.001$).

Generalized Linear Mixed Model

Across all four social groups, infant presence was not found to have a significant influence on distance to centroid and the null model was selected over the full model (Table 2). However, visually there was a slight decrease in DTC when a young infant was present (Figure

3). The social group WT stood out as being significantly different than the other three social groups in the GLMM (group [WT]: p<0.021, Table 2). The effects plot revealed that WT also had lower distances to centroid across time points and showed a different pattern of directional differences in distance to centroid in response to infant presence (Figure 4). Based on these results, WT was removed from the data set, and the tests were rerun. The results of this second test without WT (Table 3) showed significant results for infant presence affecting distance to centroid across all remaining groups (p< 0.036) and the full model was selected over the null. The plotted effects again showed a decrease in distance to centroid when a young infant was present (Figure 5).

	log_centroid_distance			
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	4.02	0.02	3.98 – 4.06	**<0.001**
young infant present [Y]	1.00	0.00	0.99 – 1.00	0.319
group [SP]	0.99	0.01	0.98 – 1.01	0.395
group [WT]	0.98	0.01	0.97 – 1.00	**0.021**
group [WW]	1.01	0.01	1.00 – 1.02	0.227
Random Effects				
σ^2	0.00			
$\tau_{00\ id}$	0.00			
$\tau_{00\ coll.month}$	0.00			
ICC	0.14			
$N_{\ id}$	26			
$N_{\ coll.month}$	9			
Observations	208			
Marginal R^2 / Conditional R^2	0.115 / 0.242			

Table 2: Generalized Linear Mixed Model for Distance to Centroid Across all Social Groups. Infant status did not show a significant effect on distance to centroid across all social groups (p<0.319). The social group Winter (WT) was significantly different than the other three social groups (p<0.021).

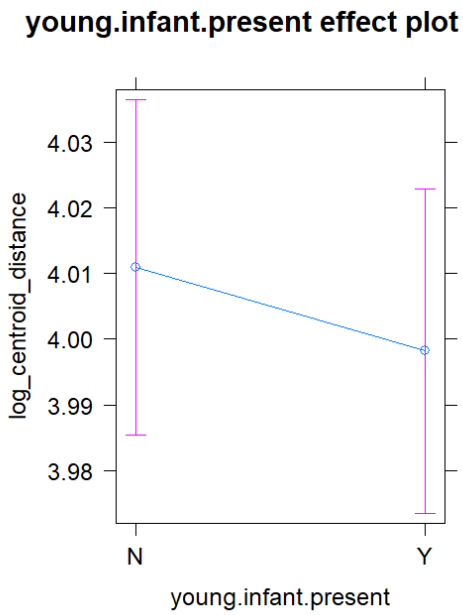


Figure 3: Effects Plot of Infant Presence on Distance to Centroid Across all Social Groups. The plotted effects of the GLMM showed a decrease in distance to centroid with a young infant present, however as seen in the GLMM results, this trend did not rise to the level of significance with all four social groups ($p<0.319$).

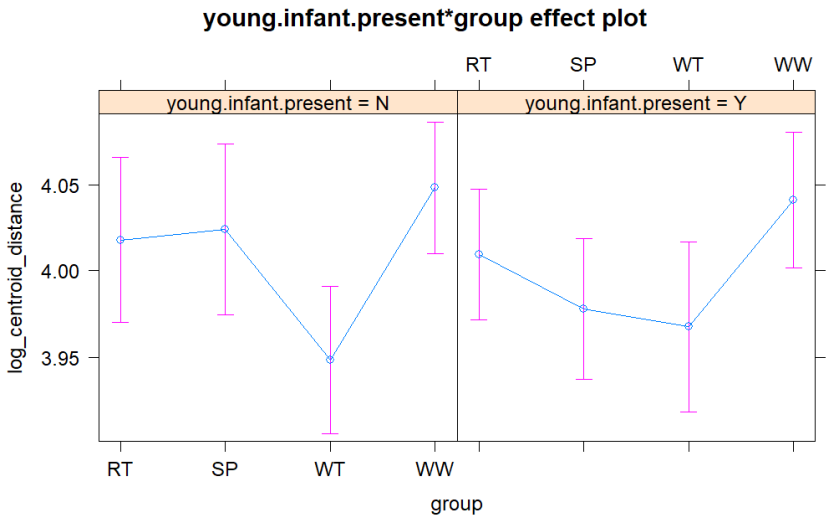


Figure 4: Effects Plot of Infant Status on Distance to Centroid Partitioned by Social Group. A visualization of the interaction between infant status and distance to centroid by social group showed that WT had an overall lower distance to centroid across time periods and showed a different pattern of directional changes in distance to centroid with a young infant present.

	log_centroid_distance			
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	4.04	0.02	4.00 – 4.07	**<0.001**
young infant present [Y]	0.99	0.00	0.99 – 1.00	**0.036**
Random Effects				
σ^2	0.00			
$\tau_{00\ id}$	0.00			
$\tau_{00\ coll.month}$	0.00			
ICC	0.28			
N_{id}	21			
$N_{coll.month}$	9			
Observations	160			
Marginal R^2 / Conditional R^2	0.023 / 0.299			

Table 3: Generalized Linear Mixed Model for Distance to Centroid without WT. With the social group WT removed, infant presence showed a significant effect on distance to centroid for the remaining three groups in the GLMM (young infant present [Y]: $p<0.036$).

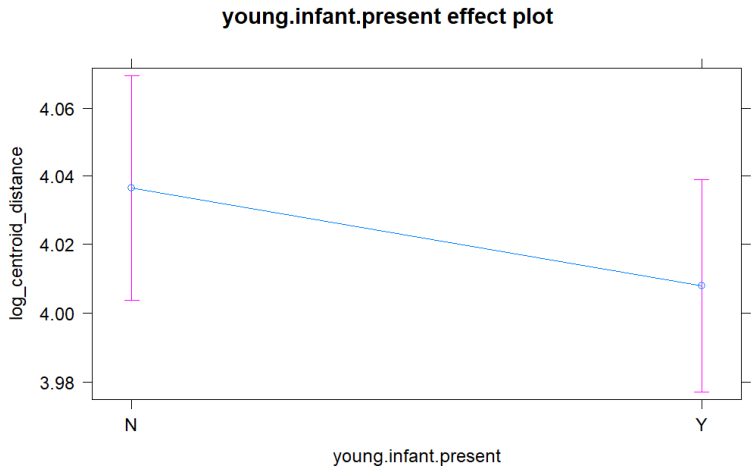
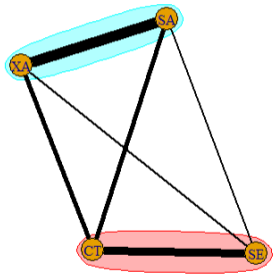


Figure 5: Effects Plot of Infant Status on Distance to Centroid without WT. With WT removed from the data set, the other three social groups showed a decrease in distance to centroid with a young infant present (young.infant.present = Y).

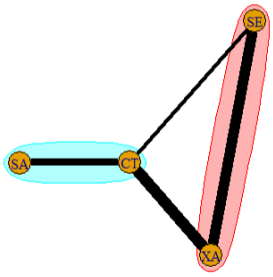
Social networks and centralization

There was not a significant difference in social cohesion between time periods with or without a young infant present across all social groups based on either metric I used for my analysis (eigenvector centralization, $p<0.152$; mean strength, $p<0.496$). Based on a visual overview, I did see structural differences with and without a young infant present in the weighted edgelist visualizations; the social groups SP and WW changed in some way between time periods whereas WT does not show such distinct changes. WT also lacked the sub structuring seen in the other social groups, visualized through differences in the color overlays (Figure 6).

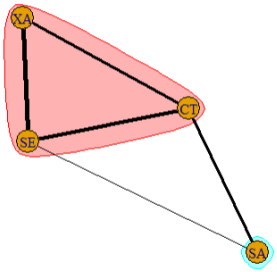
SPY1



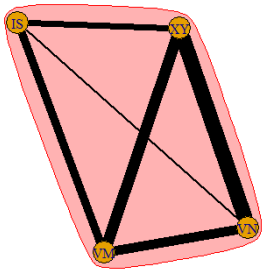
SPN1



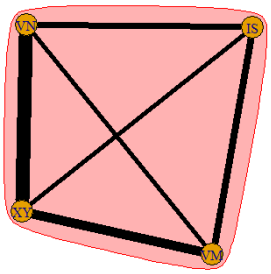
SPY2



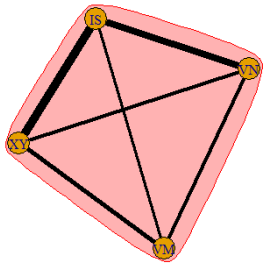
WTY1



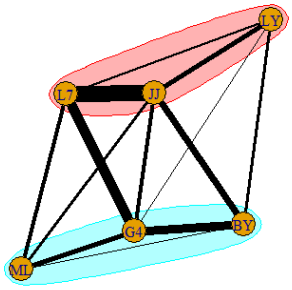
WTN1



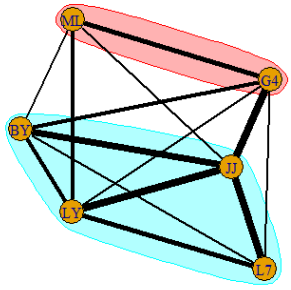
WTY2



WWY1



WWN1



WWY2

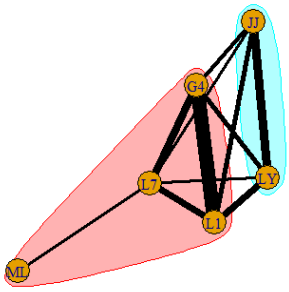


Figure 6: Weighted and Undirected Social Networks with Modularity for SP, WT, and WW. Distance matrices constructed from 1 m approaches were used to create undirected weighted edgelists with modularity analysis overlays. The edge weights denote the connection strength between individuals, and the color overlays distinguish different modules ("communities") within the network. The name of each set of matrices identifies the group (SP, WT, WW) and infant presence (Y, N). The numbers denote the time periods, differentiating between the two infant presence = Y periods, and the letters in the nodes are individuals in the group. The social group RT was excluded from the analysis as it did not have sufficient behavioral data. WT having a single-color overlay for all individuals (no sub structuring) suggested that all members in the group were closely connected.

Discussion

Infant presence influences gut microbial similarity in adult females

Through my first objective I aimed to test whether changes occurred in gut microbial composition in adult female black-and-white colobus monkeys between time periods with and without a young infant present. Using a PERMANOVA, I found significant evidence of changes in gut microbial similarity between time periods while controlling for confounding variables (collection month, field season, ID). While this analysis did reveal that the presence of an infant was having a small but significant effect on gut microbial similarity, the test was quite broad and did not indicate what change was occurring. The significant interaction between social group and infant presence in the PERMANOVA also suggested that in some way, infant status was differentially affecting gut microbial similarity between social groups.

Gut microbiomes become more similar with infant presence in most study groups

While the PERMANOVA suggested that changes in microbial similarity were indeed present across groups, I was specifically interested in testing whether the gut microbiomes of adult females in social groups became *more similar* in the presence of a young infant. Across all groups, I did not see a significant interaction between infant presence and distance to centroid in the GLMM results, suggesting that infant presence was not increasing gut microbial similarity across all social groups. However, as shown in the PERMANOVA results, it was possible that the presence of infants affected the social groups in different ways, supporting an inquiry into how certain social groups influenced the GLMM result. The GLMM results by group and the effects plot for the interaction between infant presence and distance to centroid showed that the social group Winter (WT) was different than the other three social groups. Because of this trend,

I hypothesized that WT could be disproportionately influencing the results of the GLMM, so I removed it and ran the test again. Once WT was removed, there was a significant effect of infant presence on gut microbial similarity for the remaining three social groups; the trends of WT seemed to be masking the significant results of the other groups. The plotted effects of the model excluding WT showed a decrease in distance to centroid with a young infant present, suggesting that in social groups with a young infant, the overall gut microbial compositions of the female members became more similar to each other, thus supporting hypothesis 1. It is important to interpret the results of the DTC analysis with caution; while I found evidence for an increase in gut microbial similarity with infant presence, this effect may be group or context dependent as it arose in only three out of four groups and thus requires further exploration at a group level.

No correlation between infant presence and social cohesion between groups

After finding evidence of variation in gut microbial similarity following changes in infant status, my second objective aimed to explore if this variation was in fact a result of changes in social cohesion. This idea was based on a previously documented increase in grooming with a young infant present among black-and-white colobus monkeys (Wikberg et al., 2015), and the fact that social proximity was found to be the best predictor of gut microbial similarity within the same study population (Wikberg et al., 2020). I hypothesized that when a young infant was present in a group, there would be an increase in social proximity among adult females. This could in turn facilitate increased gut microbial transmission, leading to the increase in gut microbial similarity I observed in the first part of my analysis.

I did not find a significant difference in social proximity between time periods with and without a young infant present for any of the social groups, which suggests that infant presence did not exert a significant influence on social network cohesion. This result failed to support

hypothesis 2. However, it is possible that using a 1 m proximity network was too broad of a method to evaluate changes in social cohesion; allomothering has nuances that may not have been detected within the parameters of my analyses. Research on a semi free ranging group of capuchin monkeys found that lactating females (having recently given birth) did have a larger number of grooming partners, but this did not result in significant changes in social proximity (de Lima and Ferreira, 2021). This finding suggests that although Wikberg et al. (2015) did note increases in grooming behavior with a young infant present, this does not necessarily translate to an increase in social proximity. Female black-and-white colobus monkeys are also more likely to participate in allomothering behavior with the infants of their maternal kin (Bădescu et al., 2015). These same kin members have been found to generally spend more time in close proximity within social groups independent of allomothering behavior (Wikberg et al., 2014). If the prospective allomothers and the mother were already spending time in close proximity, when an infant was born there may not have been a change in the amount of 1 m approaches between these individuals (tested in my analysis) but rather a change in the amount of direct contact via females grooming the mother to gain access to the infant as well as females grooming the infant itself (Bădescu et al., 2015; McKenna, 1979). As in other primate species, grooming on its own is likely a mediator for transmission of gut microbes in this study population with the most direct mechanism being anogenital grooming (Tung et al., 2015), however any direct contact between the mouth and hands of one individual and the fur of another could provide a means of transmission. Adult-female-to-adult-female grooming could lead to direct transmission of gut microbes. Similarly, an infant could act as a microbial reservoir and allow for an indirect source of microbial transmission between handlers.

While my statistical analyses did not detect significant changes in social cohesion, the social networks generated in igraph did show notable changes in edge weight (connection strength) and modularity (sub structuring) between time periods. These results further indicate that my evaluation of changes in social cohesion may not have been granular enough to capture changes occurring across time periods and support an investigation into other measures of social cohesion within this study population. As in the microbial analysis, WT also stood out from the other social groups, in this case because it did not show changes in sub structuring between time periods. This is consistent with the fact that WT had the most similar gut microbial compositions (lowest DTC) across time periods, and again demonstrates the need to further investigate differences between social groups.

Study group Winter (WT) is an outlier

My results for both the microbial and social network analyses suggest that WT may have experienced very different dynamics than the other three social groups during the sampling periods. At this time, it is unclear what the cause of this difference is, but it could have been due to sampling bias and/or biological differences. I checked for any variance in sampling that could have given rise to the differences seen for WT. There were no significant differences in time between sample collection or the number of samples for each group. I did find that for both the number of days and the number samples collected with a young infant present, there was unevenness across social groups, but the GLMM model fit I used for my DTC analysis has been shown to be relatively robust to uneven sampling (Pinheiro, 2014).

It is possible that there were behavioral differences between WT and the other groups that gave rise to the differences seen in my analyses. Higher overall affiliation rates within the group could drive gut microbiome homogenization, resulting in the lower overall DTC values observed

in WT and reducing the likelihood of a significant change in social structure or DTC with a young infant present. Females tend to exhibit increased rates of affiliation and grooming in periods of high stress (Cheney & Seyfarth, 2009; Engh et al., 2006; Rodrigues, 2013). If there was a threat present during time periods of data collection such as an alpha male takeover or male immigration, the females in WT may have already been spending time in close proximity. Kinship between females has also been shown to predict rates of grooming and affiliation in other primate species (Sueur et al., 2011; Tinsley Johnson et al., 2014) and it is possible that if the females in WT had a higher degree of relatedness, then they may have already been participating in higher rates of grooming and affiliation. Conversely, allomothering behavior tends to happen among related females in this population (Bădescu et al. 2015), so if WT females had a lower degree of relatedness, perhaps they displayed less allomothering behaviors, thus explaining why the presence of an infant did not have much of an effect on gut microbial similarity.

Future directions

The results of this study offer promising insight, however there is more work that needs to be done to fully explore the nuances of my study population in relation to my research question. While there were significant changes in gut microbial similarity between time periods, the change was not consistent and requires further analysis at the group level. One future direction would be evaluating WT for any biological differences compared to the other groups including kin composition or instances of high stress during the sampling period. As adult females in WT showed more similar gut microbial compositions overall (GLMM effects plot) and did not show changes in sub structuring within their group (social network visualizations)

between time periods with and without a young infant present, directly testing overall rates of affiliative behavior may be another way to help explain the differences seen in WT.

Another future direction for this work would be to evaluate social changes within groups when a young infant is present using metrics beyond 1 m approaches -- mainly grooming and infant handling. For example, it could be beneficial to create and analyze grooming rates and networks as opposed to proximity networks for each social group or weight the proximity networks with grooming rates. Future directions could also include more complex statistical approaches for determining small scale changes in social networks. Understanding the source of microbial variation seen in my data, even if it is not the same mechanism I initially proposed, would still offer insight into the role of the social environment in shaping the composition of the gut microbiome on a temporal scale.

Conclusions

The gut microbiome has gained considerable attention as a system which has important implications for many aspects of host health and function. Current research has focused on investigating how gut microbial variation effects host systems, however it is of equal importance to understand what causes gut microbial variation in the first place. I aimed to provide a more comprehensive longitudinal evaluation of how changes in social environment influence gut microbial similarity using known social changes of black-and-white colobus monkeys after the birth of an infant. I was able to find evidence of increases in gut microbial similarity during time periods with an infant present, however the effect was small and seems to be context or group dependent, motivating further investigation into the compositional and behavioral differences between social groups. This trend was also not found to be associated with any change in social proximity, and further research is required to investigate more fine-grained behavioral changes that may lead to this variation. While the means of microbial transmission was not fully revealed, this work provides insight into the temporal nature of microbial variation and builds on an understanding of how social context may influence compositional variation of the gut microbiome over time. Given the important role of the microbiome in host physiology, establishing a comprehensive understanding of the factors contributing to natural inter- and intra-individual variation could ultimately inform on strategies to investigate, maintain, and shape a healthier gut microbiome.

Supplementary Information

Ethogram

CODE	BEHAVIOR
PROXIMITY CLASSES	
0	Body contact
1	Within 1 tail length
3	Within 3 tail lengths
5	Within 5 tail lengths
A	Approach (0, 1, 3, 5)
L	Leave (0, 1, 3, 5)
CONSPECIFICS	
XX	Unidentified/unknown
XM	Unidentified male
XF	Unidentified adult female
XJ	Unidentified juvenile
XB	Unidentified infant
NM	New male
SELF DIRECTED BEHAVIORS	
AB	Defecating
AE	Piloerect
AG	Autogroom
AH	Touch
AI	Inspect
AL	Bug slap
AP	Autoplay
AS	Scratch
AU	Urinate
SAV	Scan
AV	Vigilant
AY	Yawn
DISPLAY BEHAVIOR	
DB	Stiff leg, both legs on branch **(AD L)**
DH	Display hop **(AD L)**
DI	Stiff leg, one leg only **(AD L)**
DJ	Jump display **(AD L)**
DL	Stiff leg, one leg on branch **(AD L)**
DM	Small open mouth
DO	Open mouth
DR	Run display/run through **(AD L)**
DS	Stiff leg, two legs **(AD L)**

AFFILIATIVE BEHAVIORS	
FB	Tail grab usually by infant
FC	Friendly bite (occurs within play bout) **(modifier for * FX on ipad)**
FCH	Friendly chase **(modifier for * FX on ipad)**
FF	Play face **(modifier for * FX on ipad)**
FG E	Grooming continues at end of follow
FG S	Grooming at start of follow
FG	Start groom
FGR	Friendly grab **(modifier for * FX on ipad)**
FH	Hug
FI	Inspect
FJ	(Infant) jumps on top of someone else (often when males stiff leg)
FK	Kiss, mouth to mouth, face sniff/inspect
FL	Play present **(modifier for * FX on ipad)**
FM	Grooming open mouths, not as wide as normal open mouths
FO	Over-the-head mount **(done by infants)**
FP	Groom present
FQ	Tail hit
FS	Sniff
FT	Touch (modifier *FAC*: touch to the face)
FU	Friendly pull **(modifier for * FX on ipad)**
FV	Friendly follow **(modifier for * FX on ipad)**
* FX	Play-related behaviors (modifiers include: *FC, FCH, FF, FGR, FL , FU, FV*); not a specific behavior, lumped for ease of use in recording on ipad
* FY	Friendly grapple/wrestling/bouncing in unison
AGGRESSIVE & SUBMISSIVE (Most of these will be in the Ad lib codes)	
GA	Avoid
GB	Bite
GC	Chase
GD	Displace
GE E	Aggressive end **(ADD AT THE END OF FOCAL DISPLAYS DURING CLEANING)**
GF	Flee
GG	Fear grin
GH	Hit
GJ	Bounce
GL	Lunge
GM	Moving displace **(ADD DURING CLEANING)**
GO	Cower
GP	Pounce on
GQ	Displacement but the displayed individual stays in 1m

GV	Push, shove
GR	Grab
GS	Snap at
GT	Submissive present
GU	Pull
GW	Swipe at
GX	Contact fighting
GZ	Nose grab
INFANT-RELATED BEHAVIORS	
IBC	Infant climbs on the back of another individual
ITC	Infant climbs tail of another individual
** IC	Carried
IC F	Infant is carried at start of follow
IC E	Infant carry continues as end of follow
IDF	Infant distress face; often is accompanied by squeals, infant shows and chatters teeth, usually is clearly directed towards a specific individual
** IH	Infant held
IH F	Infant being held at start of follow
IH E	Infant hold continues at end of follow
IM	Infant exploratory movement; non-directed travel, often includes bouncing; infant stays within ½ meter radius of location
IW	Infant tries to get off ventral position
IWT	Infant waves tail
ISW	Infant swings (on tail, etc.)
IA	Infant attempts access to nipple
IAV	Infant attempts to get on ventral position/initiate hold
IN F	Nursing at start of follow
** IN	Start nursing
IN E	Nursing continues at end of focal
IO	Mother attempted to get infant off nipple
IQ	Infant Squeal: Differs from VQ (vocalize squeal) in that it is by an infant and will only be used when the infant is within 5m of the mother (Modifiers include: *W: Weak or I: Intense)*
IR	Restrained, held back, transfer resisted, infant retrieved, i.e. infant pulled to body contact
IT	Infant transfer to another individual (with receiver who is the individual infant is transferred to)
	(IA/IAV) MODIFIERS
PR	Passively rejected: Preventing access to nipple (including holding arm across nipples, pulling away or turning back on infant, lying down on branch).
AR	Aggressively rejected: Following a nursing attempt involving an overt behavior such as pushing, shoving, biting, swiping, and hitting
NR	No reaction: Mother does not respond to infant's nipple access attempts

SOCIAL FOOD-RELATED BEHAVIORS	
MA	Attempted theft of food
MC	Co-feeding (feeding in the same spot, within 1 tail length or from same cluster of leaves/food patch)
MI	Mouth food
MO	Tolerated theft
MS	Steal food
MT	Touch others food
SEXUAL BEHAVIOR	
SA	Attempted mount
SD	Dismount
SE	Sex end
SJ	Ejaculate
SH	Hip touch
SI	Inspect anogenital area
SL	Sexual slap
SM	Mount
SN	Sniff anogenital area
SP	Present
SR	Resist mount
SS	Stop thrust without dismount
ST	Mount with thrust
SW	Watches sex, individual looks at couple copulating with or without interference
VOCALIZATIONS	
VA	Click-alarm call S
VC	Click before loud call
VG	Grunt (uses modifiers G, F, IG, P, IP)
	G Grunt
	F Fast grunt
	IG Intense grunt
	P Pant grunt
	IP Intense pant grunt
VH	Cough, the vocalization, not just coughing
VK	Click when open mouth
VL	Loud call
VL D	Loud call in distance (assign group if known RT WW WT SP OD AK PN etc or U unknown)
VQ	Squeal (W weak, I intense)
VR	Fight roar
VS	Scream
VY	Yelp

VX	Unknown vocalization
FOOD ITEMS	
* IL	Ingest leaf (modifiers are the trees)
IFR	Ingest fruit (modifiers are the trees)
IFL	Ingest flower (modifiers are the trees)
ISP	Ingest seedpod (modifiers are the trees)
IOT	Ingest other **(ADD DURING CLEANING)**
	AD LIB COMMENT BELOW CODES IF NECESSARY
A	Sap
B	Bark
CC	Charcoal
D	Water, drink
E	Flower bud
F	Fruit
G	Grass
H	Pith
I	Stem of the fruit
K	Stick
L	Leaf
M	Mature leaf
O	Other
P	Seed pod
Q	Leaf bud
R	Flower
S	Seed
T	Petiole
U	Bud
V	Vine
W	Wall
X	Unknown
Y	Young leaf
TRAVEL	
* TT	Start travelling
TT S	Start travelling before start of follow
TT E	Traveling continues at end of follow
TS	Small movement
TS E	Small movement continues at end of focal
OTHER ANIMALS (Modifiers following FAV)	
OO	Observer **(Receiver 0X)**
OH	Other human besides observers **(0X)**
OM	Other monkey **(Receiver is the monkey it's looking at, followed by OM)**

ZA	Automobile (includes motorcycles, tractors, cars) **(Receiver 0X)**
ZB	Bird **(Receiver 0X)**
ZC	Branch crash **(Receiver 0X)**
ZG	Pig **(Receiver 0X)**
ZM	Mona monkey **(Receiver 0X)**
ZS	Snake **(Receiver 0X)**
ZP	Sheep **(Receiver 0X)**
ZV	Look at vocalization **(Receiver 0x)**
UNK	Unknown **(Receiver 0x)**
OTHER CODES (In focals)	
OV	Out of view
OVF	Out of view face (used only when nursing possible)
IV	In view (is NOT used for face in view)
IVF	In view face
INTERGROUP (AD L)	
IS	Intergroup start
IS S	Intergroup started before observer arrived
IE	Intergroup end
IE S	Intergroup still going on when observer leave
IL	Location of encountered group or focal group if taking other location points than those scheduled on the hour **(Ad lib notes)**
IY	Activity before, during, after intergroup **(in ad lib notes)**
CI	Comments regarding intergroups or male/female incursions/excursions **(in ad lib notes)**
COMMENTS (Put in Ad lib note section with these headings)	
C	Comments general
CB	Coat color comment
CE	Comment for data editing and analyses
CF	Comment food
CI	Intergroup
CL	Location, e.g. CL 150LOW CG1 AND CG2 or CL 150AS BETWEEN CG1 AND CG2 OR Location when tree is on the map, e.g. 150DA1 – hourly & at tree changes **(PUT IN AD LIB NOTES)**
CM	Group movement, animals relative position, leader of progression
CR	Reaction to vocalizations
CV	Description of vocalizations
CW	Wounds
CX	Comment sex/consorts
CY	Comment play/games **(ad lib with infants & males)**
SHORT-CUTS	
*	Signal to yourself for data editing. (Modifiers below)

	DEL previous line
	OT other editing issue
	RR Repeat the entry from the immediately preceding line
	ST Same time as previous state
**	Dictaphone insert **(Put into Ad Lib notes section)** **MODIFIER**
POINT SAMPLES CODES	
*P	Behavior
	P FDL Feed leaves
	P FDF Feed fruit
	P FDO Feed other
	P OT Other behavior
	P OV Out of view
	P RT Rest
	P SO Social
	P SS Sexual behavior
	P TT Travel
	P VV Vigilant
*PX	Proximity of all individuals in proximity. **Click this behavior for every proximity in the point sample.**
	P0 Contact
	P1 Within 1
	P3 Within 3
	P5 Within 5
	PV Ventral
	PU Unknown proximities
*PM	Proximity to mother. **Click this behavior for every point sample.**
	P0 Contact
	P1 Within 1
	P3 Within 3
	P5 Within 5
	P+ Greater than 5 away
	PN Nursing
	PV Ventral
QUICK CLICK FOCAL KEYS (Top 15 keys)	
*	Editing key
* A	Approach
* FAV	Look at
* FX	Play-related behaviors
** IC	Infant carry
** IH	Infant handle
* IL	Ingest leaf (modifiers are the trees)

** IN	Infant nurse
* IV	In view
* L	Leave
* P	Point sample insert
* PM	Point sample mother's proximity
* PX	Point sample proximities (non-mother individuals)
* OV	Out of view
* RT	Rest
* SAV	Scan
* TT	Travel
GROUP SCAN CODES	
AG	Autogroom
IC	Infant carry (for infants only)
IH	Infant hold (for infants only)
IN	Nurse (for infants only)
FD	Feed/Foraging (Modifiers: FR – fruit, FL – flower, L – leaf, OT – other, SP – seedpod, UNK – unknown)
FG	Drink
OT	Other/unknown
RT	Rest
SA	Social aggressive behavior
SD	Social display
SF	Social friendly (affiliative other than groom)
SG	Social groom
SP	Social play
SS	Sexual behavior
SU	Submissive behavior
TT	Traveling
TV	Traveling & vigilant
VV	Vigilant, scanning long range

Supplementary Figure 1: Ethogram for all feeding and social behaviors recorded during behavioral data collection.

sample-id #q2:types	input numeric	filtered numeric	percentage of input passed filter numeric	denoised numeric	merged numeric	percentage of input merged numeric	non-chimeric numeric	percentage of input non-chimeric numeric
ADFREDOLIBPREPBLANK	473	372	78.65	303	97	20.51	97	20.51
BE_15Dec18	79607	72546	91.13	72267	68180	85.65	66944	84.09
BE_24Jul17	102536	97950	95.53	97408	93614	91.3	93333	91.02
BE_27Apr19	67411	64103	95.09	63447	60810	90.21	60738	90.1
BE_28Mar19	118440	113097	95.49	112629	109232	92.23	109192	92.19
BE_2Mar19	285	208	72.98	108	75	26.32	75	26.32
BE_31Jan19	108887	102809	94.42	102298	94198	86.51	90040	82.69
BE_3JAN19	92256	86985	94.29	86602	84510	91.6	84216	91.29
BE_6Apr18	82756	79532	96.1	79221	76088	91.94	75843	91.65
BL_13Apr18	82136	79345	96.6	79048	77280	94.09	77198	93.99
BL_14Aug17	74073	69960	94.45	69654	66478	89.75	66363	89.59
BL_14Dec18	73040	61080	83.63	60658	57721	79.03	57529	78.76
BL_26APR19	69732	62066	89.01	61472	59456	85.26	59245	84.96
BL_29Mar19	71194	67711	95.11	67406	64498	90.59	63298	88.91
BL_2MAR19	82892	77051	92.95	76796	74213	89.53	73967	89.23
BL_31Jan19	86669	81484	94.02	81029	77100	88.96	75469	87.08
BL_3Jan19	71311	67371	94.47	66933	64727	90.77	64495	90.44
BY_11Jan19	79191	74003	93.45	73609	69800	88.14	68078	85.97
BY_13Apr18	116606	112875	96.8	112499	108326	92.9	107860	92.5
BY_13Dec18	98500	93272	94.69	92951	89411	90.77	89385	90.75
BY_21Jul17	78305	73272	93.57	72689	67803	86.59	64946	82.94
BY_2May19	94225	87141	92.48	86601	78295	83.09	70179	74.48
BY_5Apr19	88229	84258	95.5	83629	78791	89.3	76819	87.07
BY_7Feb19	152178	145127	95.37	144746	137917	90.63	133322	87.61
BY_8Mar19	85432	82161	96.17	81644	77365	90.56	75725	88.64
CT_15Sep17	67306	63844	94.86	63482	60793	90.32	60474	89.85
CT_18Mar20	85248	81816	95.97	81346	76414	89.64	74188	87.03
CT_19Feb20	83924	79633	94.89	79359	76700	91.39	76137	90.72
CT_21Apr18	94982	91376	96.2	90965	87945	92.59	87701	92.33
CT_24Apr19	90605	87594	96.68	87281	84750	93.54	84389	93.14
CT_27Dec19	73669	71217	96.67	70788	68771	93.35	68568	93.08
CT_27Feb19	66817	63280	94.71	62990	60395	90.39	60232	90.14
CT_27Mar19	116420	110521	94.93	109765	99200	85.21	89871	77.2
CT_29Jan20	75837	72105	95.08	71677	69171	91.21	69016	91.01
CT_2Jan18	50193	47977	95.59	47616	44928	89.51	44107	87.87
CT_30Jan19	91394	86931	95.12	86183	78908	86.34	75674	82.8
CT_5DEC18	75408	72624	96.31	72250	69980	92.8	69347	91.96
FV_16Apr18	77725	74533	95.89	74218	72108	92.77	71964	92.59
FV_26Apr19	31908	29212	91.55	28888	27377	85.8	27266	85.45
FV_27Jul17	80849	77839	96.28	77061	73884	91.39	73629	91.07
FV_28FEB19	63408	60140	94.85	59665	57627	90.88	57260	90.3
FV_29Mar19	112096	106363	94.89	105758	102048	91.04	101578	90.62
FV_2Feb19	72483	68388	94.35	67887	65822	90.81	65390	90.21
FV_3Jan19	80968	75299	93	74651	70525	87.1	69083	85.32
FV_7Dec18	106538	97443	91.46	97101	92991	87.28	92558	86.88
G4_11JAN19	75484	72336	95.83	71837	69794	92.46	69632	92.25
G4_13Apr18	90200	86985	96.44	86609	82459	91.42	81738	90.62
G4_13Dec18	83303	79073	94.92	78424	75499	90.63	75470	90.6
G4_25Jan20	91045	87033	95.59	86469	82785	90.93	82268	90.36
G4_26Jul17	79348	75347	94.96	74958	70985	89.46	70585	88.96
G4_28Dec19	116355	111128	95.51	110568	103759	89.17	102101	87.75
G4_28Feb20	115349	110670	95.94	110297	107421	93.13	106421	92.26
G4_2MAY19	67857	64331	94.8	63977	61882	91.19	61821	91.1
G4_4Apr19	86896	83647	96.26	83219	79223	91.17	78182	89.97
G4_5MAR20	60515	58300	96.34	57946	56291	93.02	56291	93.02
G4_7Feb19	208492	198094	95.01	197475	186482	89.44	180854	86.74

G4_8Mar19	190563	175264	91.97	174640	161864	84.94	155165	81.42
IS_10Dec18	103383	99211	95.96	98641	92971	89.93	89167	86.25
IS_11Mar20	101710	98281	96.63	98007	95490	93.88	95400	93.8
IS_12Apr18	92472	90086	97.42	89757	87395	94.51	87141	94.24
IS_13Feb20	4806	4199	87.37	4100	3858	80.27	3817	79.42
IS_15Jan20	97783	84311	86.22	83829	76165	77.89	72369	74.01
IS_1Apr19	84755	82216	97	81829	78497	92.62	76483	90.24
IS_1May19	120397	115643	96.05	114955	108785	90.36	102344	85.01
IS_26Feb20	65100	61633	94.67	61222	58868	90.43	58746	90.24
IS_26Jul17	103959	101061	97.21	100615	97257	93.55	96068	92.41
IS_4Feb19	102078	95995	94.04	94885	83422	81.72	72105	70.64
IS_4MAR19	75454	72670	96.31	72358	70379	93.27	69667	92.33
IS_9Jan19	121998	117193	96.06	116765	113358	92.92	113240	92.82
JJ_11Jan19	73264	67005	91.46	66546	60566	82.67	58218	79.46
JJ_13Dec18	107281	100743	93.91	99901	89961	83.86	81133	75.63
JJ_1Feb20	97195	91135	93.77	90420	82073	84.44	77399	79.63
JJ_24Feb20	35929	33777	94.01	33466	32288	89.87	32288	89.87
JJ_26Jul17	79677	75806	95.14	75284	72555	91.06	72316	90.76
JJ_2MAY19	72231	68353	94.63	68041	65643	90.88	65453	90.62
JJ_30Dec19	85062	78703	92.52	78248	74706	87.83	74573	87.67
JJ_5Apr19	91706	88392	96.39	87772	81981	89.4	76718	83.66
JJ_5Mar20	73014	69883	95.71	69505	67147	91.96	67147	91.96
JJ_7Feb19	106764	98694	92.44	98194	91885	86.06	89907	84.21
JJ_8Mar19	85124	80729	94.84	80162	77572	91.13	77404	90.93
L1_25Jan20	86063	82204	95.52	81881	79461	92.33	79330	92.18
L1_28Dec19	76802	73907	96.23	73518	71201	92.71	71121	92.6
L1_5Feb20	90219	86115	95.45	85565	82476	91.42	82199	91.11
L1_5Mar20	5748	5087	88.5	4945	4474	77.84	4474	77.84
L7_21Mar19	102037	96878	94.94	96551	92333	90.49	92138	90.3
L7_25Jan20	146934	140821	95.84	140285	136138	92.65	135423	92.17
L7_2May19	108441	103837	95.75	103477	96761	89.23	91183	84.09
L7_30Dec19	69159	63807	92.26	63399	59227	85.64	57564	83.23
L7_5Apr19	114977	110694	96.27	110149	102740	89.36	97428	84.74
L7_5Mar20	83399	79056	94.79	78646	74478	89.3	73907	88.62
L7_6Feb20	101613	96561	95.03	96252	92765	91.29	92125	90.66
LIBBLANK1	427	341	79.86	280	136	31.85	136	31.85
LIBBLANK2	596	251	42.11	168	62	10.4	62	10.4
LIBBLANK3	328	251	76.52	161	20	6.1	20	6.1
LY_11Jan19	87623	83615	95.43	82985	78427	89.51	78104	89.14
LY_13DEC18	90120	86701	96.21	86331	84558	93.83	84558	93.83
LY_20Apr18	85692	81989	95.68	81529	77960	90.98	77830	90.83
LY_28Dec19	79019	77022	97.47	76597	74371	94.12	74189	93.89
LY_28Feb20	86465	83497	96.57	83093	81026	93.71	81001	93.68
LY_2May19	100133	96233	96.11	95607	89854	89.73	87282	87.17
LY_30Jan20	77336	74730	96.63	74194	71997	93.1	71793	92.83
LY_5APR19	77620	74399	95.85	73868	71689	92.36	71421	92.01
LY_5Mar20	81384	77629	95.39	77167	73970	90.89	73903	90.81
LY_7Feb19	79245	74527	94.05	74255	70771	89.31	70303	88.72
LY_8Mar19	120686	113817	94.31	113276	106322	88.1	102784	85.17
ML_11Jan19	73781	65555	88.85	65072	60511	82.01	59399	80.51
ML_13Apr18	100832	95394	94.61	94886	90339	89.59	89857	89.12
ML_13Dec18	160437	152662	95.15	151853	140204	87.39	129709	80.85
ML_24Feb20	74026	72031	97.31	71637	69802	94.29	69585	94
ML_25Jan20	75868	72394	95.42	71793	69388	91.46	68809	90.7
ML_2May19	132973	126086	94.82	125586	119220	89.66	118468	89.09
ML_30Dec19	83227	78031	93.76	77724	73949	88.85	73614	88.45
ML_31Jul17	93244	87138	93.45	86693	82517	88.5	81771	87.7
ML_5APR19	72727	69486	95.54	69017	66513	91.46	66238	91.08

ML_5Mar20	91656	87621	95.6	87103	85232	92.99	84691	92.4
ML_7Feb19	120820	113705	94.11	113016	105895	87.65	102159	84.55
ML_8Mar19	274	222	81.02	162	51	18.61	51	18.61
S2_18Mar20	75814	72673	95.86	72108	68613	90.5	65179	85.97
S2_19Feb20	95390	91843	96.28	91469	88720	93.01	88449	92.72
S2_27JAN20	73213	69451	94.86	69147	66878	91.35	66809	91.25
SA_13Sep17	88610	85436	96.42	85054	81489	91.96	80667	91.04
SA_18MAR20	81142	73506	90.59	72905	69624	85.81	68996	85.03
SA_19Feb20	83034	77861	93.77	77540	74918	90.23	74454	89.67
SA_21Apr18	70201	64785	92.29	64294	61529	87.65	61340	87.38
SA_24Apr19	62935	59004	93.75	58651	56768	90.2	56664	90.04
SA_27Dec19	75840	71082	93.73	70631	67979	89.63	67880	89.5
SA_27Feb19	109121	102052	93.52	101452	95740	87.74	92428	84.7
SA_27Mar19	137069	128375	93.66	127785	118329	86.33	109213	79.68
SA_29Jan20	88601	82984	93.66	82577	80206	90.52	80206	90.52
SA_2Jan18	81791	76508	93.54	76037	73805	90.24	73652	90.05
SA_30Jan19	394	327	82.99	247	116	29.44	116	29.44
SA_5Dec18	75916	70089	92.32	69329	66935	88.17	66831	88.03
SE_17Aug17	79726	76869	96.42	76396	73361	92.02	72945	91.49
SE_17Feb20	100498	96380	95.9	95847	93840	93.37	93656	93.19
SE_18MAR20	98052	83837	85.5	83406	79768	81.35	79499	81.08
SE_24APR19	73828	71254	96.51	70960	69546	94.2	69297	93.86
SE_27Dec19	75982	67272	88.54	66867	63754	83.91	63177	83.15
SE_27FEB19	87664	73698	84.07	73132	69765	79.58	69576	79.37
SE_27Jan20	94814	88214	93.04	87767	85400	90.07	85195	89.85
SE_27Mar19	93525	83449	89.23	82904	77192	82.54	75085	80.28
SE_2Jan18	75264	70205	93.28	69680	67180	89.26	66988	89
SE_30Jan19	107923	96593	89.5	96088	90688	84.03	89626	83.05
SE_5Dec18	84099	73324	87.19	72217	65292	77.64	62217	73.98
SU_13Apr18	108910	104833	96.26	104237	100027	91.84	98041	90.02
SU_24Jul17	95400	90590	94.96	90082	87438	91.65	87162	91.36
SU_27APR19	81893	78426	95.77	77795	75721	92.46	75517	92.21
SU_28Feb19	97626	93067	95.33	92424	87813	89.95	85606	87.69
SU_29Mar19	61600	56785	92.18	56259	53640	87.08	53330	86.57
SU_31Jan19	94287	89747	95.18	89307	83760	88.84	81460	86.4
SU_31Jan20	79988	75466	94.35	75067	72180	90.24	71816	89.78
SU_3Jan19	82048	76047	92.69	75679	72275	88.09	71530	87.18
SU_7Dec18	95236	90314	94.83	89685	84484	88.71	82969	87.12
T8_24Feb20	91217	86818	95.18	86382	83536	91.58	83264	91.28
T9_3Aug17	92751	89268	96.24	88853	85705	92.4	85080	91.73
TE_11Apr18	78598	75680	96.29	75412	72880	92.73	72610	92.38
TE_17Aug17	85268	82008	96.18	81545	78884	92.51	78601	92.18
TE_26Apr19	117175	111251	94.94	110697	106257	90.68	102360	87.36
TE_28Feb19	59423	57659	97.03	57407	55694	93.72	55608	93.58
TE_28Mar19	82453	79017	95.83	78686	74117	89.89	73289	88.89
TE_31Jan19	114737	107956	94.09	107433	101757	88.69	100108	87.25
TE_3Jan19	67974	64801	95.33	64375	61448	90.4	60707	89.31
TE_7Dec18	105726	93734	88.66	92868	81473	77.06	71853	67.96
U1_8Feb20	89676	84469	94.19	84116	81046	90.38	80631	89.91
UG_11May18	389	318	81.75	251	135	34.7	135	34.7
UG_24Jul17	64644	60874	94.17	60395	57645	89.17	57464	88.89
UG_26APR19	66694	60566	90.81	60372	58676	87.98	58422	87.6
UG_28Feb19	87621	80915	92.35	80506	76903	87.77	75954	86.68
UG_29Mar19	80315	74215	92.4	73746	69666	86.74	68823	85.69
UG_3Jan19	93484	89670	95.92	89182	84796	90.71	83323	89.13
UG_4Feb19	11778	10365	88	10130	9357	79.44	9357	79.44
UG_8Dec18	80704	74027	91.73	73547	69555	86.19	68357	84.7
V8_18Mar20	112363	107297	95.49	106724	98405	87.58	92101	81.97

V8_4Mar20	96898	92915	95.89	92400	88895	91.74	88351	91.18
VM_10DEC18	77050	74629	96.86	74272	72888	94.6	72842	94.54
VM_13FEB20	71448	68058	95.26	67627	66253	92.73	65399	91.53
VM_15JAN20	75740	69390	91.62	69128	66552	87.87	66229	87.44
VM_16Dec19	78077	75410	96.58	74847	71697	91.83	71202	91.19
VM_1Apr19	131071	126936	96.85	126469	121447	92.66	118928	90.74
VM_1May19	71280	69162	97.03	68911	66358	93.09	65751	92.24
VM_3Aug17	115692	111925	96.74	111493	107144	92.61	106017	91.64
VM_4Feb19	92572	88471	95.57	88104	83456	90.15	81140	87.65
VM_4Mar19	111067	107012	96.35	106668	103552	93.23	102508	92.29
VM_7Apr18	62377	60361	96.77	60079	58031	93.03	57975	92.94
VM_9Jan19	95134	90921	95.57	90289	85586	89.96	82664	86.89
VM_9Mar20	44852	42249	94.2	42017	40317	89.89	40233	89.7
VN_10Dec18	122215	116462	95.29	115749	108307	88.62	100334	82.1
VN_11Jan19	98715	95195	96.43	94892	92511	93.72	92310	93.51
VN_11Mar20	81612	78066	95.66	77784	75114	92.04	74947	91.83
VN_12Apr18	75876	73567	96.96	73336	71695	94.49	71695	94.49
VN_13FEB20	95193	92295	96.96	92094	90651	95.23	90293	94.85
VN_15JAN20	97211	89108	91.66	88811	85921	88.39	85824	88.29
VN_18Dec19	84147	81217	96.52	80905	78169	92.9	77974	92.66
VN_1Apr19	93267	89512	95.97	89145	86116	92.33	85844	92.04
VN_1May19	169684	164422	96.9	163610	153125	90.24	140539	82.82
VN_4Feb19	110455	107178	97.03	106737	102521	92.82	98365	89.05
VN_4Mar19	90492	87682	96.89	87466	86050	95.09	84184	93.03
VN_5Aug17	102056	98477	96.49	97860	90332	88.51	85403	83.68
VN_7Aug17	72749	69931	96.13	69565	67169	92.33	67020	92.12
XA_10MAY18	71189	68327	95.98	67898	65954	92.65	65738	92.34
XA_19Feb20	112435	107600	95.7	106986	96655	85.97	90910	80.86
XA_21Sep17	83238	80342	96.52	79772	73477	88.27	69759	83.81
XA_24APR19	121922	118850	97.48	118614	116907	95.89	116615	95.65
XA_27DEC19	54534	52866	96.94	52577	50825	93.2	50791	93.14
XA_27Feb19	90290	86970	96.32	86451	82177	91.01	78074	86.47
XA_27JAN20	69878	66890	95.72	66516	64904	92.88	64904	92.88
XA_27Mar19	102594	97253	94.79	96595	88003	85.78	82019	79.95
XA_2Jan18	157070	149949	95.47	149207	138413	88.12	132742	84.51
XA_30Jan19	75982	72553	95.49	71994	66479	87.49	64486	84.87
XA_5Dec18	65451	63035	96.31	62603	60510	92.45	60376	92.25
XY_10Dec18	985	829	84.16	703	362	36.75	362	36.75
XY_11Jan19	57409	55338	96.39	55094	52548	91.53	52413	91.3
XY_12Feb20	80117	76210	95.12	75772	73133	91.28	72189	90.1
XY_15JAN20	83919	78655	93.73	78400	76461	91.11	76327	90.95
XY_16Dec19	88617	85321	96.28	84839	82140	92.69	81930	92.45
XY_19Apr18	132266	127412	96.33	127104	120798	91.33	117153	88.57
XY_1Apr19	95370	90407	94.8	90053	86712	90.92	86480	90.68
XY_1May19	95499	90529	94.8	89904	80634	84.43	71640	75.02
XY_26Jul17	110939	105896	95.45	105342	98606	88.88	95570	86.15
XY_4Feb19	106055	102133	96.3	101763	94143	88.77	88425	83.38
XY_4Mar19	104717	100929	96.38	100630	96542	92.19	94866	90.59
XY_9Mar20	80584	76400	94.81	75804	69686	86.48	65069	80.75

Supplementary Figure 2: Summary statistics after denoising and quality filtering with DADA2 in QIIME2.

sample.id	name	PCR.plate	sample_or	group	coll.year	year.int	coll.month	month.group	month.int	dataset	young.infant.present	num.infants	fecaltimepoint	fieldseasor
ADFREDOLIBPREP	adfbsaprepblank	P4	control	NA	NA	NA	NA	NA	NA	BSA	NA	NA	NA	NA
LIBBLANK3	LIBBLANK3	P3	control	NA	NA	NA	NA	NA	NA	ORIGINAL	NA	NA	NA	NA
BE_24Jul17	BE	P1	sample	RT	SEVENTEEI		17 JUL	C		7 ORIGINAL	N		0 RT1	0.5
BE_27Apr19	BE	P1	sample	RT	NINETEEN		19 APR	B		4 ORIGINAL	N		0 RT8	1
BE_6Apr18	BE	P2	sample	RT	EIGHTEEN		18 APR	B		4 ORIGINAL	N		0 RT2	0.75
BE_28Mar19	BE	P2	sample	RT	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 RT7	1
BE_15Dec18	BE	P1	sample	RT	EIGHTEEN		18 DEC	A		12 ORIGINAL	Y		2 RT3	1
BE_2Mar19	BE	P2	sample	RT	NINETEEN		19 MAR	B		3 ORIGINAL	Y		2 RT6	1
BE_3JAN19	BE	P4	sample	RT	NINETEEN		19 JAN	A		1 BSA	Y		2 RT4	1
BE_31Jan19	BE	P1	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		3 RT5	1
BL_13Apr18	BL	P2	sample	RT	EIGHTEEN		18 APR	B		4 ORIGINAL	N		0 RT2	0.75
BL_14Aug17	BL	P1	sample	RT	SEVENTEEI		17 AUG	C		8 ORIGINAL	N		0 RT1	0.5
BL_26APR19	BL	P4	sample	RT	NINETEEN		19 APR	B		4 BSA	N		0 RT8	1
BL_29Mar19	BL	P2	sample	RT	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 RT7	1
BL_14Dec18	BL	P1	sample	RT	EIGHTEEN		18 DEC	A		12 ORIGINAL	Y		2 RT3	1
BL_2MAR19	BL	P4	sample	RT	NINETEEN		19 MAR	B		3 BSA	Y		2 RT6	1
BL_3Jan19	BL	P2	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		2 RT4	1
BL_31Jan19	BL	P3	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		3 RT5	1
FV_16Apr18	FV	P3	sample	RT	EIGHTEEN		18 APR	B		4 ORIGINAL	N		0 RT2	0.75
FV_26Apr19	FV	P1	sample	RT	NINETEEN		19 APR	B		4 ORIGINAL	N		0 RT8	1
FV_27Jul17	FV	P2	sample	RT	SEVENTEEI		17 JUL	C		7 ORIGINAL	N		0 RT1	0.5
FV_29Mar19	FV	P2	sample	RT	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 RT7	1
FV_7Dec18	FV	P1	sample	RT	EIGHTEEN		18 DEC	A		12 ORIGINAL	Y		1 RT3	1
FV_28FEB19	FV	P4	sample	RT	NINETEEN		19 FEB	A		2 BSA	Y		2 RT6	1
FV_3Jan19	FV	P1	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		2 RT4	1
FV_2Feb19	FV	P2	sample	RT	NINETEEN		19 FEB	A		2 ORIGINAL	Y		3 RT5	1
SU_13Apr18	SU	P3	sample	RT	EIGHTEEN		18 APR	B		4 ORIGINAL	N		0 RT2	0.75
SU_24Jul17	SU	P1	sample	RT	SEVENTEEI		17 JUL	C		7 ORIGINAL	N		0 RT1	0.5
SU_27APR19	SU	P4	sample	RT	NINETEEN		19 APR	B		4 BSA	N		0 RT8	1
SU_29Mar19	SU	P2	sample	RT	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 RT7	1
SU_7Dec18	SU	P1	sample	RT	EIGHTEEN		18 DEC	A		12 ORIGINAL	Y		1 RT3	1
SU_28Feb19	SU	P2	sample	RT	NINETEEN		19 FEB	A		2 ORIGINAL	Y		2 RT6	1
SU_3Jan19	SU	P2	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		2 RT4	1
SU_31Jan19	SU	P1	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		3 RT5	1
SU_31Jan20	SU	P1	sample	RT	TWENTY		20 JAN	A		1 ORIGINAL	Y		3 RT9	2
T8_24Feb20	T8	P1	sample	RT	TWENTY		20 FEB	A		2 ORIGINAL	Y		1 RT9	2
TE_11Apr18	TE	P2	sample	RT	EIGHTEEN		18 APR	B		4 ORIGINAL	N		0 RT2	0.75
TE_17Aug17	TE	P1	sample	RT	SEVENTEEI		17 AUG	C		8 ORIGINAL	N		0 RT1	0.5
TE_26Apr19	TE	P2	sample	RT	NINETEEN		19 APR	B		4 ORIGINAL	N		0 RT8	1
TE_28Mar19	TE	P2	sample	RT	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 RT7	1
TE_7Dec18	TE	P3	sample	RT	EIGHTEEN		18 DEC	A		12 ORIGINAL	Y		1 RT3	1
TE_28Feb19	TE	P2	sample	RT	NINETEEN		19 FEB	A		2 ORIGINAL	Y		2 RT6	1
TE_3Jan19	TE	P2	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		2 RT4	1
TE_31Jan19	TE	P1	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		3 RT5	1
U1_8Feb20	U1	P3	sample	RT	TWENTY		20 FEB	A		2 ORIGINAL	Y		2 RT9	2
UG_11May18	UG	P2	sample	RT	EIGHTEEN		18 MAY	B		5 ORIGINAL	N		0 RT2	0.75
UG_24Jul17	UG	P1	sample	RT	SEVENTEEI		17 JUL	C		7 ORIGINAL	N		0 RT1	0.5
UG_26APR19	UG	P4	sample	RT	NINETEEN		19 APR	B		4 ORIGINAL	N		0 RT8	1
UG_29Mar19	UG	P3	sample	RT	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 RT7	1
UG_8Dec18	UG	P2	sample	RT	EIGHTEEN		18 DEC	A		12 ORIGINAL	Y		1 RT3	1
UG_28Feb19	UG	P2	sample	RT	NINETEEN		19 FEB	A		2 ORIGINAL	Y		2 RT6	1
UG_3Jan19	UG	P1	sample	RT	NINETEEN		19 JAN	A		1 ORIGINAL	Y		2 RT4	1
UG_4Feb19	UG	P2	sample	RT	NINETEEN		19 FEB	A		2 ORIGINAL	Y		3 RT5	1
CT_21Apr18	CT	P2	sample	SP	EIGHTEEN		18 APR	B		4 ORIGINAL	N		0 SP2	0.75
CT_27Dec19	CT	P1	sample	SP	NINETEEN		19 DEC	A		12 ORIGINAL	N		0 SP9	2
CT_2Jan18	CT	P3	sample	SP	NINETEEN		19 JAN	A		1 ORIGINAL	N		0 SP4	1
CT_5DEC18	CT	P4	sample	SP	EIGHTEEN		18 DEC	A		12 BSA	N		0 SP3	1
CT_19Feb20	CT	P1	sample	SP	TWENTY		20 FEB	A		2 ORIGINAL	Y		1 SP11	2
CT_24Apr19	CT	P1	sample	SP	NINETEEN		19 APR	B		4 ORIGINAL	Y		1 SP8	1
CT_27Mar19	CT	P1	sample	SP	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 SP7	1
CT_29Jan20	CT	P1	sample	SP	TWENTY		20 JAN	A		1 ORIGINAL	Y		1 SP10	2
CT_18Mar20	CT	P1	sample	SP	TWENTY		20 MAR	B		3 ORIGINAL	Y		2 SP12	2
CT_27Feb19	CT	P2	sample	SP	NINETEEN		19 FEB	A		2 ORIGINAL	Y		2 SP6	1
CT_30Jan19	CT	P3	sample	SP	NINETEEN		19 JAN	A		1 ORIGINAL	Y		2 SP5	1
CT_15Sep17	CT	P2	sample	SP	SEVENTEEI		17 SEP	D		9 ORIGINAL	Y		3 SP1	0.5
S2_19Feb20	S2	P1	sample	SP	TWENTY		20 FEB	A		2 ORIGINAL	Y		1 SP11	2
S2_27JAN20	S2	P4	sample	SP	TWENTY		20 JAN	A		1 BSA	Y		1 SP10	2
S2_18Mar20	S2	P1	sample	SP	TWENTY		20 MAR	B		3 ORIGINAL	Y		2 SP12	2
SA_21Apr18	SA	P3	sample	SP	EIGHTEEN		18 APR	B		4 ORIGINAL	N		0 SP2	0.75
SA_27Dec19	SA	P2	sample	SP	NINETEEN		19 DEC	A		12 ORIGINAL	N		0 SP9	2
SA_2Jan18	SA	P2	sample	SP	NINETEEN		19 JAN	A		1 ORIGINAL	N		0 SP4	1
SA_5Dec18	SA	P2	sample	SP	EIGHTEEN		18 DEC	A		12 ORIGINAL	N		0 SP3	1
SA_19Feb20	SA	P2	sample	SP	TWENTY		20 FEB	A		2 ORIGINAL	Y		1 SP11	2
SA_24Apr19	SA	P2	sample	SP	NINETEEN		19 APR	B		4 ORIGINAL	Y		1 SP8	1
SA_27Mar19	SA	P2	sample	SP	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 SP7	1
SA_29Jan20	SA	P1	sample	SP	TWENTY		20 JAN	A		1 ORIGINAL	Y		1 SP10	2
SA_18MAR20	SA	P4	sample	SP	TWENTY		20 MAR	B		3 BSA	Y		2 SP12	2
SA_27Feb19	SA	P3	sample	SP	NINETEEN		19 FEB	A		2 ORIGINAL	Y		2 SP6	1
SA_30Jan19	SA	P2	sample	SP	NINETEEN		19 JAN	A		1 ORIGINAL	Y		2 SP5	1
SA_13Sep17	SA	P2	sample	SP	SEVENTEEI		17 SEP	D		9 ORIGINAL	Y		3 SP1	0.5
SE_17Aug17	SE	P2	sample	SP	SEVENTEEI		17 AUG	C		8 ORIGINAL	N		0 SP1	0.5
SE_27Dec19	SE	P2	sample	SP	NINETEEN		19 DEC	A		12 ORIGINAL	N		0 SP9	2
SE_2Jan18	SE	P3	sample	SP	NINETEEN		19 JAN	A		1 ORIGINAL	N		0 SP4	1
SE_5Dec18	SE	P2	sample	SP	EIGHTEEN		18 DEC	A		12 ORIGINAL	N		0 SP3	1
SE_17Feb20	SE	P2	sample	SP	TWENTY		20 FEB	A		2 ORIGINAL	Y		1 SP11	2
SE_24APR19	SE	P4	sample	SP	NINETEEN		19 APR	B		4 BSA	Y		1 SP8	1
SE_27Jan20	SE	P1	sample	SP	TWENTY		20 JAN	A		1 ORIGINAL	Y		1 SP10	2
SE_27Mar19	SE	P2	sample	SP	NINETEEN		19 MAR	B		3 ORIGINAL	Y		1 SP7	1
SE_18MAR20	SE	P4	sample	SP	TWENTY		20 MAR	B		3 BSA	Y		2 SP12	2

SE_27FEB19	SE	P4	sample	SP	NINETEEN	19	FEB	A	2	BSA	Y	2	SP6	1
SE_30Jan19	SE	P2	sample	SP	NINETEEN	19	JAN	A	1	ORIGINAL	Y	2	SP5	1
T9_3Aug17	T9	P1	sample	SP	SEVENTEEI	17	AUG	C	8	ORIGINAL	N	0	SP1	0.5
XA_27DEC19	XA	P4	sample	SP	NINETEEN	19	DEC	A	12	BSA	N	0	SP9	2
XA_2Jan18	XA	P3	sample	SP	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	SP4	1
XA_5Dec18	XA	P2	sample	SP	EIGHTEEN	18	DEC	A	12	ORIGINAL	N	0	SP3	1
XA_10MAY18	XA	P4	sample	SP	EIGHTEEN	18	MAY	B	5	BSA	N	0	SP2	0.75
XA_19Feb20	XA	P1	sample	SP	TWENTY	20	FEB	A	2	ORIGINAL	Y	1	SP11	2
XA_24APR19	XA	P4	sample	SP	NINETEEN	19	APR	B	4	BSA	Y	1	SP8	1
XA_27JAN20	XA	P4	sample	SP	TWENTY	20	JAN	A	1	BSA	Y	1	SP10	2
XA_27Mar19	XA	P2	sample	SP	NINETEEN	19	MAR	B	3	ORIGINAL	Y	1	SP7	1
XA_27Feb19	XA	P2	sample	SP	NINETEEN	19	FEB	A	2	ORIGINAL	Y	2	SP6	1
XA_30Jan19	XA	P2	sample	SP	NINETEEN	19	JAN	A	1	ORIGINAL	Y	2	SP5	1
XA_21Sep17	XA	P1	sample	SP	SEVENTEEI	17	SEP	D	9	ORIGINAL	Y	3	SP1	0.5
IS_10Dec18	IS	P3	sample	WT	EIGHTEEN	18	DEC	A	12	ORIGINAL	N	0	WT3	1
IS_11Mar20	IS	P1	sample	WT	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WT13	2
IS_12Apr18	IS	P3	sample	WT	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WT2	0.75
IS_13Feb20	IS	P1	sample	WT	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WT11	2
IS_26Feb20	IS	P1	sample	WT	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WT11	2
IS_26Jul17	IS	P1	sample	WT	SEVENTEEI	17	JUL	C	7	ORIGINAL	N	0	WT1	0.5
IS_4Feb19	IS	P1	sample	WT	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WT5	1
IS_9Jan19	IS	P1	sample	WT	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WT4	1
IS_15Jan20	IS	P2	sample	WT	TWENTY	20	JAN	A	1	ORIGINAL	Y	1	WT10	2
IS_1Apr19	IS	P2	sample	WT	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WT7	1
IS_1May19	IS	P2	sample	WT	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WT8	1
IS_4MAR19	IS	P4	sample	WT	NINETEEN	19	MAR	B	3	BSA	Y	1	WT6	1
V8_18Mar20	V8	P2	sample	WT	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WT13	2
V8_4Mar20	V8	P2	sample	WT	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WT12	2
VM_10DEC18	VM	P4	sample	WT	EIGHTEEN	18	DEC	A	12	BSA	N	0	WT3	1
VM_13FEB20	VM	P4	sample	WT	TWENTY	20	FEB	A	2	BSA	N	0	WT11	2
VM_3Aug17	VM	P1	sample	WT	SEVENTEEI	17	AUG	C	8	ORIGINAL	N	0	WT1	0.5
VM_4Feb19	VM	P1	sample	WT	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WT5	1
VM_7Apr18	VM	P3	sample	WT	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WT2	0.75
VM_9Jan19	VM	P3	sample	WT	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WT4	1
VM_9Mar20	VM	P2	sample	WT	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WT13	2
VM_15JAN20	VM	P4	sample	WT	TWENTY	20	JAN	A	1	BSA	Y	1	WT10	2
VM_16Dec19	VM	P1	sample	WT	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WT9	2
VM_1Apr19	VM	P2	sample	WT	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WT7	1
VM_1May19	VM	P3	sample	WT	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WT8	1
VM_4Mar19	VM	P2	sample	WT	NINETEEN	19	MAR	B	3	ORIGINAL	Y	1	WT6	1
VN_10Dec18	VN	P2	sample	WT	EIGHTEEN	18	DEC	A	12	ORIGINAL	N	0	WT3	1
VN_11Jan19	VN	P2	sample	WT	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WT4	1
VN_11Mar20	VN	P1	sample	WT	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WT13	2
VN_12Apr18	VN	P3	sample	WT	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WT2	0.75
VN_13FEB20	VN	P4	sample	WT	TWENTY	20	FEB	A	2	BSA	N	0	WT11	2
VN_4Feb19	VN	P1	sample	WT	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WT5	1
VN_5Aug17	VN	P1	sample	WT	SEVENTEEI	17	AUG	C	8	ORIGINAL	N	0	WT1	0.5
VN_7Aug17	VN	P1	sample	WT	SEVENTEEI	17	AUG	C	8	ORIGINAL	N	0	WT1	0.5
VN_15JAN20	VN	P4	sample	WT	TWENTY	20	JAN	A	1	BSA	Y	1	WT10	2
VN_18Dec19	VN	P2	sample	WT	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WT9	2
VN_1Apr19	VN	P2	sample	WT	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WT7	1
VN_1May19	VN	P1	sample	WT	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WT8	1
VN_4Mar19	VN	P2	sample	WT	NINETEEN	19	MAR	B	3	ORIGINAL	Y	1	WT6	1
XY_10Dec18	XY	P3	sample	WT	EIGHTEEN	18	DEC	A	12	ORIGINAL	N	0	WT3	1
XY_11Jan19	XY	P3	sample	WT	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WT4	1
XY_12Feb20	XY	P1	sample	WT	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WT11	2
XY_19Apr18	XY	P3	sample	WT	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WT2	0.75
XY_26Jul17	XY	P1	sample	WT	SEVENTEEI	17	JUL	C	7	ORIGINAL	N	0	WT1	0.5
XY_4Feb19	XY	P2	sample	WT	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WT5	1
XY_9Mar20	XY	P1	sample	WT	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WT13	2
XY_15JAN20	XY	P4	sample	WT	TWENTY	20	JAN	A	1	BSA	Y	1	WT10	2
XY_16Dec19	XY	P2	sample	WT	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WT9	2
XY_1Apr19	XY	P2	sample	WT	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WT7	1
XY_1May19	XY	P1	sample	WT	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WT8	1
XY_4Mar19	XY	P1	sample	WT	NINETEEN	19	MAR	B	3	ORIGINAL	Y	1	WT6	1
BY_11Jan19	BY	P1	sample	WW	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WW4	1
BY_13Apr18	BY	P2	sample	WW	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WW2	0.75
BY_21Jul17	BY	P2	sample	WW	SEVENTEEI	17	JUL	C	7	ORIGINAL	N	0	WW1	0.5
BY_8Mar19	BY	P1	sample	WW	NINETEEN	19	MAR	B	3	ORIGINAL	N	0	WW6	1
BY_7Feb19	BY	P2	sample	WW	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WW5	1
BY_13Dec18	BY	P1	sample	WW	EIGHTEEN	18	DEC	A	12	ORIGINAL	Y	1	WW3	1
BY_2May19	BY	P2	sample	WW	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WW8	1
BY_5Apr19	BY	P2	sample	WW	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WW7	1
G4_11JAN19	G4	P4	sample	WW	NINETEEN	19	JAN	A	1	BSA	N	0	WW4	1
G4_13Apr18	G4	P2	sample	WW	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WW2	0.75
G4_26Jul17	G4	P1	sample	WW	SEVENTEEI	17	JUL	C	7	ORIGINAL	N	0	WW1	0.5
G4_28Feb20	G4	P1	sample	WW	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WW11	2
G4_5MAR20	G4	P4	sample	WW	TWENTY	20	MAR	B	3	BSA	N	0	WW12	2
G4_7Feb19	G4	P1	sample	WW	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WW5	1
G4_8Mar19	G4	P1	sample	WW	NINETEEN	19	MAR	B	3	ORIGINAL	N	0	WW6	1
G4_13Dec18	G4	P1	sample	WW	EIGHTEEN	18	DEC	A	12	ORIGINAL	Y	1	WW3	1
G4_25Jan20	G4	P1	sample	WW	TWENTY	20	JAN	A	1	ORIGINAL	Y	1	WW10	2
G4_28Dec19	G4	P1	sample	WW	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WW9	2
G4_2MAY19	G4	P4	sample	WW	NINETEEN	19	MAY	B	5	BSA	Y	1	WW8	1
G4_4Apr19	G4	P2	sample	WW	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WW7	1
JJ_11Jan19	JJ	P2	sample	WW	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WW4	1
JJ_24Feb20	JJ	P1	sample	WW	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WW11	2
JJ_26Jul17	JJ	P1	sample	WW	SEVENTEEI	17	JUL	C	7	ORIGINAL	N	0	WW1	0.5
JJ_5Mar20	JJ	P1	sample	WW	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WW12	2
JJ_7Feb19	JJ	P2	sample	WW	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WW5	1
JJ_8Mar19	JJ	P2	sample	WW	NINETEEN	19	MAR	B	3	ORIGINAL	N	0	WW6	1
JJ_13Dec18	JJ	P3	sample	WW	EIGHTEEN	18	DEC	A	12	ORIGINAL	Y	1	WW3	1

JJ_1Feb20	JJ	P1	sample	WW	TWENTY	20	FEB	A	2	ORIGINAL	Y	1	WW10	2
JJ_2MAY19	JJ	P4	sample	WW	NINETEEN	19	MAY	B	5	BSA	Y	1	WW8	1
JJ_30Dec19	JJ	P2	sample	WW	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WW9	2
JJ_5Apr19	JJ	P2	sample	WW	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WW7	1
L1_5Mar20	L1	P1	sample	WW	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WW12	2
L1_5Feb20	L1	P1	sample	WW	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WW11	2
L1_25Jan20	L1	P1	sample	WW	TWENTY	20	JAN	A	1	ORIGINAL	Y	1	WW10	2
L1_28Dec19	L1	P2	sample	WW	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WW9	2
L7_5Mar20	L7	P1	sample	WW	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WW12	2
L7_6Feb20	L7	P1	sample	WW	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WW11	2
L7_25Jan20	L7	P1	sample	WW	TWENTY	20	JAN	A	1	ORIGINAL	Y	1	WW10	2
L7_2May19	L7	P1	sample	WW	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WW8	1
L7_30Dec19	L7	P2	sample	WW	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WW9	2
L7_5Apr19	L7	P3	sample	WW	NINETEEN	19	APR	B	4	ORIGINAL	Y	1	WW7	1
LY_11Jan19	LY	P2	sample	WW	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WW4	1
LY_20Apr18	LY	P2	sample	WW	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WW2	0.75
LY_28Feb20	LY	P1	sample	WW	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WW11	2
LY_5Mar20	LY	P1	sample	WW	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WW12	2
LY_7Feb19	LY	P1	sample	WW	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WW5	1
LY_8Mar19	LY	P3	sample	WW	NINETEEN	19	MAR	B	3	ORIGINAL	N	0	WW6	1
LY_13DEC18	LY	P4	sample	WW	EIGHTEEN	18	DEC	A	12	BSA	Y	1	WW3	1
LY_28Dec19	LY	P2	sample	WW	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WW9	2
LY_2May19	LY	P1	sample	WW	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WW8	1
LY_30Jan20	LY	P2	sample	WW	TWENTY	20	JAN	A	1	ORIGINAL	Y	1	WW10	2
LY_5APR19	LY	P4	sample	WW	NINETEEN	19	APR	B	4	BSA	Y	1	WW7	1
ML_11Jan19	ML	P1	sample	WW	NINETEEN	19	JAN	A	1	ORIGINAL	N	0	WW4	1
ML_13Apr18	ML	P2	sample	WW	EIGHTEEN	18	APR	B	4	ORIGINAL	N	0	WW2	0.75
ML_24Feb20	ML	P2	sample	WW	TWENTY	20	FEB	A	2	ORIGINAL	N	0	WW11	2
ML_31Jul17	ML	P1	sample	WW	SEVENTEEI	17	JUL	C	7	ORIGINAL	N	0	WW1	0.5
ML_5Mar20	ML	P2	sample	WW	TWENTY	20	MAR	B	3	ORIGINAL	N	0	WW12	2
ML_7Feb19	ML	P1	sample	WW	NINETEEN	19	FEB	A	2	ORIGINAL	N	0	WW5	1
ML_8Mar19	ML	P1	sample	WW	NINETEEN	19	MAR	B	3	ORIGINAL	N	0	WW6	1
ML_13Dec18	ML	P1	sample	WW	EIGHTEEN	18	DEC	A	12	ORIGINAL	Y	1	WW3	1
ML_25Jan20	ML	P2	sample	WW	TWENTY	20	JAN	A	1	ORIGINAL	Y	1	WW10	2
ML_2May19	ML	P2	sample	WW	NINETEEN	19	MAY	B	5	ORIGINAL	Y	1	WW8	1
ML_30Dec19	ML	P2	sample	WW	NINETEEN	19	DEC	A	12	ORIGINAL	Y	1	WW9	2
ML_5APR19	ML	P4	sample	WW	NINETEEN	19	APR	B	4	BSA	Y	1	WW7	1

Supplementary Figure 3: Metadata sheet used for statistical analyses. Pertinent columns added to the original metadata sheet include infant presence (young.infant.present), number of infants (num.infants), fecal time point, and field season. Sample ID refers to the name of the individual that the fecal sample was taken from as well as when it was taken.

Bibliography

Abt, M. C., & Pamer, E. G. (2014). Commensal bacteria mediated defenses against pathogens. *Current Opinion in Immunology*, *29*, 16–22. https://doi.org/10.1016/j.coi.2014.03.003

Amabebe, E., Robert, F. O., Agbalalah, T., & Orubu, E. S. F. (2020). Microbial dysbiosis-induced obesity: Role of gut microbiota in homoeostasis of energy metabolism. *British Journal of Nutrition*, *123*(10), 1127–1137. https://doi.org/10.1017/S0007114520000380

Amato, K. R., Van Belle, S., Di Fiore, A., Estrada, A., Stumpf, R., White, B., Nelson, K. E., Knight, R., & Leigh, S. R. (2017). Patterns in Gut Microbiota Similarity Associated with Degree of Sociality among Sex Classes of a Neotropical Primate. *Microbial Ecology*, *74*(1), 250–258. https://doi.org/10.1007/s00248-017-0938-6

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral ecology*, *26*(1), 32-46.

Archie, E. A., & Theis, K. R. (2011). Animal behaviour meets microbial ecology. *Animal Behaviour*, *82*(3), 425–436. https://doi.org/10.1016/j.anbehav.2011.05.029

Bădescu, I., Sicotte, P., Ting, N., & Wikberg, E. C. (2015). Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*): Infant Handling in *Colobus*. *American Journal of Primatology*, *77*(4), 376–387. https://doi.org/10.1002/ajp.22353

Bennett, G., Malone, M., Sauther, M. L., Cuozzo, F. P., White, B., Nelson, K. E., Stumpf, R. M., Knight, R., Leigh, S. R., & Amato, K. R. (2016). Host age, social group, and habitat type influence the gut microbiota of wild ring-tailed lemurs (Lemur catta). American Journal of Primatology, 78(8), 883–892. https://doi.org/10.1002/ajp.22555

Bittinger K (2020). usedist: Distance Matrix Utilities. R package version 0.4.0, https://CRAN.R-project.org/package=usedist.

Bisanz, J (2018). "qiime2R: Importing QIIME2 artifacts and associated data into R sessions." https://github.com/jbisanz/qiime2R

Bjork, J. R., Dasari, M., Grieneisen, L., & Archie, E. A. (2019). Primate microbiomes over time: Longitudinal answers to standing questions in microbiome research. *American Journal of Primatology*, *81*(10–11). https://doi.org/10.1002/ajp.22970

Bolyen E, Rideout JR, Dillon MR, Bokulich NA, Abnet CC, Al-Ghalith GA, Alexander H, Alm EJ, Arumugam M, Asnicar F, Bai Y, Bisanz JE, Bittinger K, Brejnrod A, Brislawn CJ, Brown CT, Callahan BJ, Caraballo-Rodríguez AM, Chase J, Cope EK, Da Silva R, Diener C, Dorrestein PC, Douglas GM, Durall DM, Duvallet C, Edwardson CF, Ernst M, Estaki M, Fouquier J, Gauglitz JM, Gibbons SM, Gibson DL, Gonzalez A, Gorlick K, Guo J, Hillmann B, Holmes S, Holste H, Huttenhower C, Huttley GA, Janssen S, Jarmusch AK, Jiang L, Kaehler BD, Kang KB, Keefe CR, Keim P, Kelley ST, Knights

D, Koester I, Kosciolek T, Kreps J, Langille MGI, Lee J, Ley R, Liu YX, Loftfield E, Lozupone C, Maher M, Marotz C, Martin BD, McDonald D, McIver LJ, Melnik AV, Metcalf JL, Morgan SC, Morton JT, Naimey AT, Navas-Molina JA, Nothias LF, Orchanian SB, Pearson T, Peoples SL, Petras D, Preuss ML, Pruesse E, Rasmussen LB, Rivers A, Robeson MS, Rosenthal P, Segata N, Shaffer M, Shiffer A, Sinha R, Song SJ, Spear JR, Swafford AD, Thompson LR, Torres PJ, Trinh P, Tripathi A, Turnbaugh PJ, Ul-Hasan S, van der Hooft JJJ, Vargas F, Vázquez-Baeza Y, Vogtmann E, von Hippel M, Walters W, Wan Y, Wang M, Warren J, Weber KC, Williamson CHD, Willis AD, Xu ZZ, Zaneveld JR, Zhang Y, Zhu Q, Knight R, and Caporaso JG. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nature Biotechnology 37: 852–857. https://doi.org/10.1038/s41587-019-0209-9

Brandes, U., Delling, D., Gaertler, M., Gorke, R., Hoefer, M., Nikoloski, Z., & Wagner, D. (2008). On Modularity Clustering. IEEE Transactions on Knowledge and Data Engineering, 20(2), 172–188. https://doi.org/10.1109/TKDE.2007.190689

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017). "glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling." *The R Journal*, **9**(2), 378–400. doi:10.32614/RJ-2017-066.

Bukin, Y. S., Galachyants, Y. P., Morozov, I. V., Bukin, S. V., Zakharenko, A. S., & Zemskaya, T. I. (2019). The effect of 16S rRNA region choice on bacterial community metabarcoding results. *Scientific Data*, *6*(1), Article 1. https://doi.org/10.1038/sdata.2019.7

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: High resolution sample inference from Illumina amplicon data. *Nature Methods*, *13*(7), 581–583. https://doi.org/10.1038/nmeth.3869

Caruso, R., Ono, M., Bunker, M. E., Núñez, G., & Inohara, N. (2019). Dynamic and Asymmetric Changes of the Microbial Communities after Cohousing in Laboratory Mice. *Cell Reports*, *27*(11), 3401-3412.e3. https://doi.org/10.1016/j.celrep.2019.05.042

Cheney, D. L., & Seyfarth, R. M. (2009). Chapter 1 Stress and Coping Mechanisms in Female Primates. In *Advances in the Study of Behavior* (Vol. 39, pp. 1–44). Elsevier. https://doi.org/10.1016/S0065-3454(09)39001-4

Clapp, M., Aurora, N., Herrera, L., Bhatia, M., Wilen, E., & Wakefield, S. (2017). Gut Microbiota's Effect on Mental Health: The Gut-Brain Axis. *Clinics and Practice*, *7*(4), 987. https://doi.org/10.4081/cp.2017.987

Csardi G, Nepusz T (2006). "The igraph software package for complex network research." *InterJournal*, Complex Systems, 1695. https://igraph.org.

de Lima, V. C. C., & Ferreira, R. G. (2021). Social network changes during the development of immature capuchin monkeys (Sapajus spp.). *Primates*, *62*(5), 801–815. https://doi.org/10.1007/s10329-021-00918-6

Degnan, P. H., Pusey, A. E., Lonsdorf, E. V., Goodall, J., Wroblewski, E. E., Wilson, M. L., Rudicell, R. S., Hahn, B. H., & Ochman, H. (2012). Factors associated with the diversification of the gut microbial communities within chimpanzees from Gombe National Park. *Proceedings of the National Academy of Sciences*, *109*(32), 13034–13039. https://doi.org/10.1073/pnas.1110994109

Dill-McFarland, K. A., Tang, Z.-Z., Kemis, J. H., Kerby, R. L., Chen, G., Palloni, A., Sorenson, T., Rey, F. E., & Herd, P. (2019). Close social relationships correlate with human gut microbiota composition. *Scientific Reports*, *9*(1), 703. https://doi.org/10.1038/s41598-018-37298-9

Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., & Cheney, D. L. (2006). Behavioural and hormonal responses to predation in female chacma baboons (Papio hamadryas ursinus). *Proceedings of the Royal Society B: Biological Sciences*, *273*(1587), 707–712. https://doi.org/10.1098/rspb.2005.3378

Ezenwa, V. O., Ghai, R. R., McKay, A. F., & Williams, A. E. (2016). Group living and pathogen infection revisited. *Current Opinion in Behavioral Sciences*, *12*, 66–72. https://doi.org/10.1016/j.cobeha.2016.09.006

Fox J (2003). "Effect Displays in R for Generalised Linear Models." Journal of Statistical Software, 8(15), 1–27. doi:10.18637/jss.v008.i15.

Fox J, Weisberg S (2019). An R Companion to Applied Regression, 3rd edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/index.html.

Gacesa, R., Kurilshikov, A., Vich Vila, A., Sinha, T., Klaassen, M. A. Y., Bolte, L. A., Andreu-Sánchez, S., Chen, L., Collij, V., Hu, S., Dekens, J. A. M., Lenters, V. C., Björk, J. R., Swarte, J. C., Swertz, M. A., Jansen, B. H., Gelderloos-Arends, J., Jankipersadsing, S., Hofker, M., … Weersma, R. K. (2022). Environmental factors shaping the gut microbiome in a Dutch population. *Nature*, *604*(7907), 732–739. https://doi.org/10.1038/s41586-022-04567-7

Gloor, G. B., Macklaim, J. M., Pawlowsky-Glahn, V., & Egozcue, J. J. (2017). Microbiome datasets are compositional: and this is not optional. *Frontiers in microbiology*, *8*, 2224.

Gomez, A., Petrzelkova, K., Yeoman, C. J., Vlckova, K., Mrázek, J., Koppova, I., Carbonero, F., Ulanov, A., Modry, D., Todd, A., Torralba, M., Nelson, K. E., Gaskins, H. R., Wilson, B., Stumpf, R. M., White, B. A., & Leigh, S. R. (2015). Gut microbiome composition and metabolomic profiles of wild western lowland gorillas (*Gorilla gorilla gorilla*) reflect host ecology. *Molecular Ecology*, *24*(10), 2551–2565. https://doi.org/10.1111/mec.13181

Goodfellow, C. K., Whitney, T., Christie, D. M., Sicotte, P., Wikberg, E. C., & Ting, N. (2019). Divergence in gut microbial communities mirrors a social group fission event in a black-and-white colobus monkey (*Colobus vellerosus*). *American Journal of Primatology*, *81*(10–11). https://doi.org/10.1002/ajp.22966

Grieneisen, L. E., Livermore, J., Alberts, S., Tung, J., & Archie, E. A. (2017). Group Living and Male Dispersal Predict the Core Gut Microbiome in Wild Baboons. *Integrative and Comparative Biology*, *57*(4), 770–785. https://doi.org/10.1093/icb/icx046

Hanneman, R. A., & Riddle, M. (2005). Introduction to social network methods. Riverside: University of California, Riverside.

Hooper, L. V., Littman, D. R., & Macpherson, A. J. (2012). Interactions Between the Microbiota and the Immune System. *Science*, *336*(6086), 1268–1273. https://doi.org/10.1126/science.1223490

Hsiao, E. Y., McBride, S. W., Hsien, S., Sharon, G., Hyde, E. R., McCue, T., Codelli, J. A., Chow, J., Reisman, S. E., Petrosino, J. F., Patterson, P. H., & Mazmanian, S. K. (2013). Microbiota Modulate Behavioral and Physiological Abnormalities Associated with Neurodevelopmental Disorders. *Cell*, *155*(7), 1451–1463. https://doi.org/10.1016/j.cell.2013.11.024

Jena, A., Montoya, C. A., Mullaney, J. A., Dilger, R. N., Young, W., McNabb, W. C., & Roy, N. C. (2020). Gut-Brain Axis in the Early Postnatal Years of Life: A Developmental Perspective. *Frontiers in Integrative Neuroscience*, *14*, 44. https://doi.org/10.3389/fnint.2020.00044

Kankam, B. O., & Sicotte, P. (2013). The Effect of Forest Fragment Characteristics on Abundance of Colobus vellerosus in the Forest-Savanna Transition Zone of Ghana. *Folia Primatologica*, *84*(2), 74–86. https://doi.org/10.1159/000348307

Kelly, J. R., Borre, Y., O' Brien, C., Patterson, E., El Aidy, S., Deane, J., Kennedy, P. J., Beers, S., Scott, K., Moloney, G., Hoban, A. E., Scott, L., Fitzgerald, P., Ross, P., Stanton, C., Clarke, G., Cryan, J. F., & Dinan, T. G. (2016). Transferring the blues: Depression-associated gut microbiota induces neurobehavioural changes in the rat. *Journal of Psychiatric Research*, *82*, 109–118. https://doi.org/10.1016/j.jpsychires.2016.07.019

Koch, H., & Schmid-Hempel, P. (2011). Socially transmitted gut microbiota protect bumble bees against an intestinal parasite. *Proceedings of the National Academy of Sciences*, *108*(48), 19288–19292. https://doi.org/10.1073/pnas.1110474108

Lahti L, Shetty S (2017). Tools for microbiome analysis in R. Microbiome package version 1.19.1, http://microbiome.github.com/microbiome.

Lax, S., Smith, D. P., Hampton-Marcell, J., Owens, S. M., Handley, K. M., Scott, N. M., Gibbons, S. M., Larsen, P., Shogan, B. D., Weiss, S., Metcalf, J. L., Ursell, L. K., Vázquez-Baeza, Y., Van Treuren, W., Hasan, N. A., Gibson, M. K., Colwell, R., Dantas, G., Knight, R., & Gilbert, J. A. (2014). Longitudinal analysis of microbial interaction between humans and the indoor environment. *Science (New York, N.Y.)*, *345*(6200), 1048–1052. https://doi.org/10.1126/science.1254529

Li, W.-Z., Stirling, K., Yang, J.-J., & Zhang, L. (2020). Gut microbiota and diabetes: From correlation to causality and mechanism. *World Journal of Diabetes*, *11*(7), 293–308. https://doi.org/10.4239/wjd.v11.i7.293

Lombardo, M. P. (2008). Access to mutualistic endosymbiotic microbes: An underappreciated benefit of group living. *Behavioral Ecology and Sociobiology*, *62*(4), 479–497. https://doi.org/10.1007/s00265-007-0428-9

McKenna, J. J. (1979). The Evolution of Allomothering Behavior among Colobine Monkeys: Function and Opportunism in Evolution. *American Anthropologist*, *81*(4), 818–840. https://doi.org/10.1525/aa.1979.81.4.02a00040

McMurdie PJ, Holmes S (2013). "phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data." *PLoS ONE*, 8(4), e61217. http://dx.plos.org/10.1371/journal.pone.0061217.

Moeller, A. H., Foerster, S., Wilson, M. L., Pusey, A. E., Hahn, B. H., & Ochman, H. (2016). Social behavior shapes the chimpanzee pan-microbiome. *Science Advances*, *2*(1), e1500997. https://doi.org/10.1126/sciadv.1500997

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly, M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). vegan: Community Ecology Package. R package version 2.6-2, https://CRAN.R-project.org/package=vegan.

Perofsky, A. C., Ancel Meyers, L., Abondano, L. A., Di Fiore, A., & Lewis, R. J. (2021). Social groups constrain the spatiotemporal dynamics of wild sifaka gut microbiomes. *Molecular Ecology*, *30*(24), 6759–6775. https://doi.org/10.1111/mec.16193

Perofsky, A. C., Lewis, R. J., Abondano, L. A., Di Fiore, A., & Meyers, L. A. (2017). Hierarchical social networks shape gut microbial composition in wild Verreaux's sifaka. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1868), 20172274. https://doi.org/10.1098/rspb.2017.2274

Pinheiro, J. C. (2014). Linear mixed effects models for longitudinal data. Wiley StatsRef: Statistics Reference Online

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., & Glöckner, F. O. (2013). The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic acids research, 41(Database issue), D590–D596. https://doi.org/10.1093/nar/gks1219

Quinn, T. P., Erb, I., Richardson, M. F., & Crowley, T. M. (2018). Understanding sequencing data as compositions: An outlook and review. *Bioinformatics*, *34*(16), 2870–2878. https://doi.org/10.1093/bioinformatics/bty175

Radjabzadeh, D., Bosch, J. A., Uitterlinden, A. G., Zwinderman, A. H., Ikram, M. A., van Meurs, J. B. J., Luik, A. I., Nieuwdorp, M., Lok, A., van Duijn, C. M., Kraaij, R., & Amin, N. (2022). Gut microbiome-wide association study of depressive symptoms. *Nature Communications*, *13*(1), 7128. https://doi.org/10.1038/s41467-022-34502-3

Raulo, A., Ruokolainen, L., Lane, A., Amato, K., Knight, R., Leigh, S., Stumpf, R., White, B., Nelson, K. E., Baden, A. L., & Tecot, S. R. (2018). Social behaviour and gut microbiota in red-bellied lemurs (Eulemur rubriventer): In search of the role of immunity in the evolution of sociality. *Journal of Animal Ecology*, *87*(2), 388–399. https://doi.org/10.1111/1365-2656.12781

Ren, T., Grieneisen, L. E., Alberts, S. C., Archie, E. A., & Wu, M. (2016). Development, diet and dynamism: Longitudinal and cross-sectional predictors of gut microbial communities in wild baboons: Gut microbiota in wild baboons. *Environmental Microbiology*, *18*(5), 1312–1325. https://doi.org/10.1111/1462-2920.12852

Rodrigues, M. A. (2013). *Stress and sociality in a patrilocal primate: Do female spider monkeys tend-and-befriend?* (Doctoral dissertation, The Ohio State University).

Rudolph, K., Schneider, D., Fichtel, C., Daniel, R., Heistermann, M., & Kappeler, P. M. (2022). Drivers of gut microbiome variation within and between groups of a wild Malagasy primate. *Microbiome*, *10*(1), 28. https://doi.org/10.1186/s40168-021-01223-6

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Song, S. J., Lauber, C., Costello, E. K., Lozupone, C. A., Humphrey, G., Berg-Lyons, D., Caporaso, J. G., Knights, D., Clemente, J. C., Nakielny, S., Gordon, J. I., Fierer, N., & Knight, R. (2013). Cohabiting family members share microbiota with one another and with their dogs. *ELife*, *2*, e00458. https://doi.org/10.7554/eLife.00458

Springer, A., Fichtel, C., Al-Ghalith, G. A., Koch, F., Amato, K. R., Clayton, J. B., Knights, D., & Kappeler, P. M. (2017). Patterns of seasonality and group membership characterize the gut microbiota in a longitudinal study of wild Verreaux's sifakas (*Propithecus verreauxi*). *Ecology and Evolution*, *7*(15), 5732–5745. https://doi.org/10.1002/ece3.3148

Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*(4), 845–852. https://doi.org/10.1016/j.anbehav.2011.07.020

Suzuki, T. A. (2017). Links between Natural Variation in the Microbiome and Host Fitness in Wild Mammals. *Integrative and Comparative Biology*, *57*(4), 756–769. https://doi.org/10.1093/icb/icx104

Tavalire, H. F., Christie, D. M., Leve, L. D., Ting, N., Cresko, W. A., & Bohannan, B. J. M. (2021). Shared Environment and Genetics Shape the Gut Microbiome after Infant Adoption. *MBio*, *12*(2), e00548-21. https://doi.org/10.1128/mBio.00548-21

Teichroeb, J. A., Saj, T. L., Paterson, J. D., & Sicotte, P. (2003). Effect of Group Size on Activity Budgets of Colobus vellerosus in Ghana. *International Journal of Primatology*.

Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2014). Kinship and Dominance Rank Influence the Strength of Social Bonds in Female Geladas (Theropithecus gelada). *International Journal of Primatology*, *35*(1), 288–304. https://doi.org/10.1007/s10764-013-9733-5

Tung, J., Barreiro, L. B., Burns, M. B., Grenier, J.-C., Lynch, J., Grieneisen, L. E., Altmann, J., Alberts, S. C., Blekhman, R., & Archie, E. A. (2015). Social networks predict gut microbiome composition in wild baboons. *ELife*, *4*, e05224. https://doi.org/10.7554/eLife.05224

Valles-Colomer, M., Blanco-Míguez, A., Manghi, P., Asnicar, F., Dubois, L., Golzato, D., Armanini, F., Cumbo, F., Huang, K. D., Manara, S., Masetti, G., Pinto, F., Piperni, E., Punčochář, M., Ricci, L., Zolfo, M., Farrant, O., Goncalves, A., Selma-Royo, M., … Segata, N. (2023). The person-to-person transmission landscape of the gut and oral microbiomes. *Nature*, *614*(7946), 125–135. https://doi.org/10.1038/s41586-022-05620-1

Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

Wikberg, E. C., Christie, D., Sicotte, P., & Ting, N. (2020). Interactions between social groups of colobus monkeys (Colobus vellerosus) explain similarities in their gut microbiomes. *Animal Behaviour*, *163*, 17–31. https://doi.org/10.1016/j.anbehav.2020.02.011

Wikberg, E. C., Ting, N., & Sicotte, P. (2014). Kinship and similarity in residency status structure female social networks in black-and-white colobus monkeys (colobus vellerosus): SOCIAL NETWORKS IN FEMALE *COLOBUS VELLEROSUS*. *American Journal of Physical Anthropology*, *153*(3), 365–376. https://doi.org/10.1002/ajpa.22435

Wikberg, E. C., Ting, N., & Sicotte, P. (2015). Demographic Factors Are Associated with Intergroup Variation in the Grooming Networks of Female Colobus (Colobus vellerosus). *International Journal of Primatology*, *36*(1), 124–142. https://doi.org/10.1007/s10764-015-9816-6

Wong, S. N. P., & Sicotte, P. (2006). Population size and density of Colobus vellerosus at the Boabeng-Fiema Monkey Sanctuary and surrounding forest fragments in Ghana. *American Journal of Primatology*, *68*(5), 465–476. https://doi.org/10.1002/ajp.20242