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Investigating Social Preferences in a High Fission-Fusion Society of Black and White Ruffed Lemur (Varecia Variegata)

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Investigating Social Preferences in a High Fission-Fusion Society of Black and White Ruffed Lemur *(Varecia Variegata)*

by

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ABSTRACT

Ruffed lemur *(Varecia variegata)* are primates that show strong social preferences. It is not known, however, if these preferences are associated with specific behaviors. The current study investigates a wild community of ruffed lemur in Ranomafana National Park, Madagascar, and tested for social preferences across six behaviors: rest, feed/forage, travel, mutual grooming, play, and aggression. Results demonstrate that the grouping patterns of ruffed lemur are highly conservative across these behaviors, despite the unstable fission-fusion patterns typical of their social organization. Using a social network analysis model, we calculated 53,000 scans representing 40 individuals and their associated activity states and asked - does an individual tend to do certain behaviors (e.g., rest) in the proximity of one associate (nearest-neighbor) but different behaviors (e.g., feed) with others? Dyadic associations were plotted on network graphs across behavioral states, and the networks with the largest sample size were used to test for consistency in the networks of the rare behaviors. We observed consistent groupings of animals across all networks, including the rare social behaviors. Further, in all networks, we observed a low average number of nearest-neighbor present with a focal animal. Our results demonstrate that ruffed lemur display highly conservative social preferences, which are highly consistent across behavioral states, despite high fission fusion traits. This finding lays the foundation for using nearest-neighbor network graphs as a proxy of social preference for future endeavors.

INTRODUCTION

It can be said that prosociality is central to human success as a species. Traits such as empathy, cooperation, and trust for example, allow humans to survive in large societies across the globe (Ehlert et al. 2020). Yet, many aspects of human social behavior have an evolutionary origin starting with our closest primate relatives – chimpanzees and bonobos (Warneken et al. 2014).

We can generally define social behavior as that which is directed toward or takes place between two or more members of the same species (Amdam et al., 2011). The behavior choices an animal makes and their consequences are what characterize social preferences (Sueur et al., 2011). Being socially avoidant can be costly for species as defending territory, cooperative hunting and allomaternal care, for example can increase a species' probability of survival. Social networks of a group of conspecifics can influence individual and collective behaviors which can not only affect evolutionary outcomes but can also be an important consideration in conservation applications and management as they relate to long-term factors such as population genetics and gene flow, spatial pattern and use of range, and overall degree of species' fitness (Baden et al 2020; Sutherland 1998; Wilson 1971, 1975). Understanding social preferences as a way of addressing these conservation concerns may help to mitigate long lasting detrimental effects.

Madagascar is one of the five most biodiverse conservation hotspots in the world (Myers et al. 2000). It is home to five lemur families that constitute more than twenty percent of the globe's primate species and which are the most threatened group of mammals in the world (Schweitzer et al., 2014). Black-and-white ruffed lemurs (*varecia*

variegata) are arboreal frugivores endemic to the island where they are classified as critically endangered on the IUCN's red-list due to poaching and habitat fragmentation and loss (Louis et al. 2020); and, where nearly fifty percent of the island's forest is now positioned within less than three hundred and twenty-eight feet (or one-hundred meters) from the forest edge (Vieilledent et al. 2018).

While most primates live in cohesive social groups, where preferences can often be constrained by who the group members are, research has shown that ruffed lemurs are predominantly found in more flexible bands where individuals come and go. Baden et al. (2016) noted that no community members were ever found together in 16+ consecutive months of data collection; individuals spent nearly fifty percent of their time alone or in subgroups that were highly variable in size (2-10+) and composition. This high variability was usually due to changes in season, fruit availability & reproductive state. They also found low rates of association in this female-oriented society. White & Balko et al (1993) have also maintained that lemur organization is highly variable and can range from lemurs living in pairs to bigger groupings of multi male and multi female. These flexible grouping patterns of high fission-fusion societies may allow for enhanced variation in social preferences to emerge in these ruffed lemur communities.

In a follow up study in 2020, Baden et al., explored the factors shaping these variable association patterns in ruffed lemur and determined that the preferences were related to the animal's ranging behaviors and not to kinship (as it is for some taxa). Some variation remained unexplained, however, and this drew attention to the animal's use of space and gradations of behavior specific to the individual and overall species as necessary supplemental factors when examining social preference and association.

This led to my investigation of the presence of social preferences in this same community of free-living black and white ruffed lemur in Mangevo, Madagascar. As the previous study focused on group composition as a way to determine preference among associates, I chose to use nearest-neighbor of the focal animal as a proxy for preference. I defined nearest-neighbor as the animal closest to the focal individual while the focal was observed practicing any of the six behavioral states that we explored that are part of the suite of ranging behaviors typical of these animals.

RESEARCH AIMS

Using social network analysis, I examined the networks of the animals across the behavioral categories of rest, feed/forage, travel, mutual grooming, play and aggression. I examined network structure as it pertained to each behavior and compared networks to ascertain trends. I examined whether the animals were staying together across behavioral states or if social preferences varied with these behavioral states.

METHODS

Study Site and Subjects

Data were collected from one *V. variegata* community at Mangevo in Ranomafana National Park, Madagascar (RNP) by the Baden Primate Molecular Ecology Lab at Hunter College and a team of six research technicians as part of the Ranomafana Ruffed Lemur Project in Mangevo, Ranomafana National Park, Madagascar. Data were collected over a 27-month period (September 2017 – December 2019). Mangevo [21º22'60''S, 47º28'0''E] is a mid-elevation (660-1,200m)

primary rainforest site that is located in the southeastern parcel of RNP, **(Fig. 1, 2)**

containing 435km^2 of continuous montane rainforest located in the southeastern

escarpment of Madagascar's central high plateau [21º02'-21º25'S and 47º18'-47º 37'E;

Wright et al., 2012] (Baden et al., 2016).

All individuals in this study were habituated to observer presence and had been

individually identified via radio-collars and/or unique collar-tag combinations prior to the

behavioral observations conducted (see Baden et al., 2016 for details). Animals were

collared following a strict protocol previously outlined under veterinary supervision

(Glander,1993).

Permission for research was granted by and research protocols were in

compliance with Hunter College IACUC # AB-lemurs 5/20-01 and Madagascar's

National Parks (MNP 63/17, 152/18, 092/19, 395/19 /MEEF/SG/DGF/DSAP/SCB.Re.).

Principles for the Ethical Treatment of Non-Human Primates were adhered to as set

forth by the American Society of Primatologists (ASP).
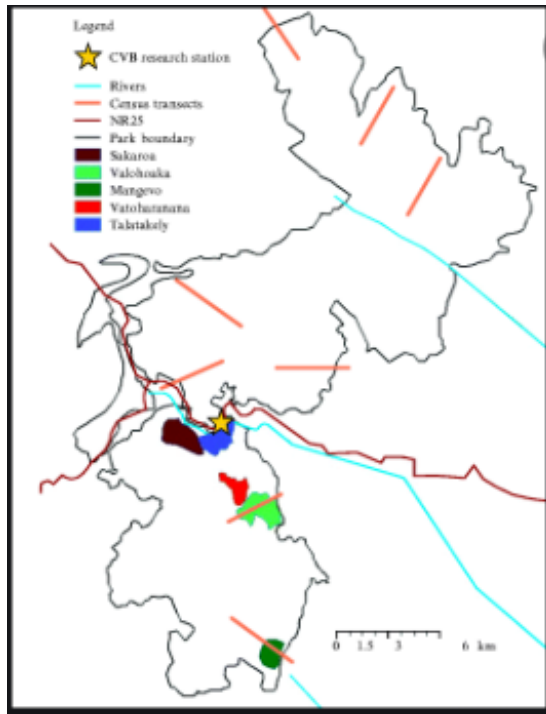
Figure 1. Map shows study site from which data were collected in Mangevo in Ranomafana National Park, Madagascar as part of the long-term Ranomafana Ruffed Lemur Project (Wright et al., 2012).
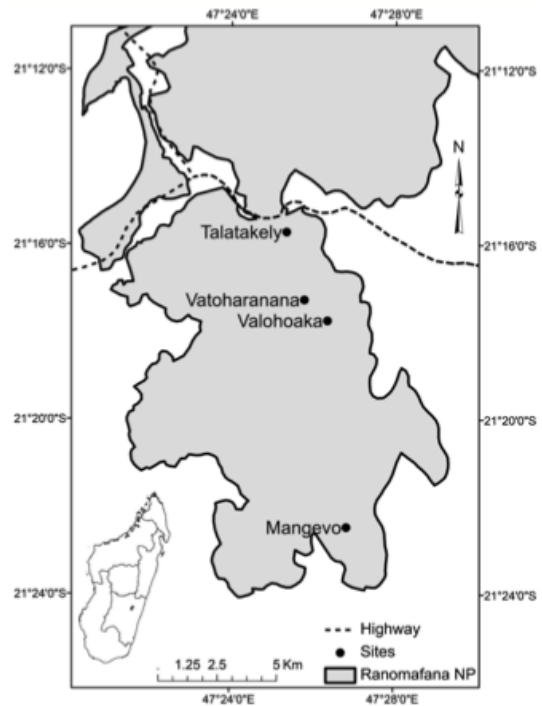
Figure 2. Map shows an amplified view of Mangevo with coordinates in RNP (Razafindratsima et al., 2014).

Data Collection

Behavioral monitoring

Data were collected on both the focal animal and the animal closest to the focal animal (the nearest-neighbor) in dawn to dusk follows that were conducted daily by two teams of four observers. Using radiotelemetry to locate a focal animal to follow at the beginning of each observation period, new focals were selected to follow each day (the same focal was never sampled on two consecutive days) and each focal was followed at least once per month. (Baden, et. al. 2016)

Five-minute instantaneous group scans were conducted during the daily observation periods, which lasted between 8 and 11 hours long. The exact timeframe was often dependent on the length of daylight which varied according to season as well as on how long it took to locate a focal animal at dawn. Only focal animals with radio-collars were considered for this study however it was noted when a focal was present with a non-collared nearest-neighbor, as were the collared and non-collared individuals present in the group's composition.

Upon locating a focal animal, the individual identities, age, and sex of all other individuals present within the subgroup, were also recorded, as was their proximity. While performing the 5-minute instantaneous scan sampling, any changes in subgroup conformation, structure, and size as well as the activity state of the focal subject throughout the day were noted (Baden et al., 2020).

If individuals were within 50m of the group center, they were considered members of a subgroup if they were seen to be associating with (traveling or in close vicinity to) members of the subgroup being followed. While average group distribution for this ruffed lemur population had previously been described as being between 6m and 15m (it seldom surpassed 30m), subgroup spread here was habitually much smaller though 50m was used as a boundary (Baden et al., 2020).

Sampling efforts resulted in a total of **4,320** focal observation hours. For the purposes of this study, we focused our analyses on six behavior types: rest, feed/forage, travel, mutual grooming, play, and aggression. Nearest-neighbor was defined as the animal closest to the focal individual when the focal was performing a behavior. Of the 53,298 instantaneous scans recorded, a total of 48,171 focal follows

with nearest-neighbor were included and analyzed. This represents a total animal count of 40 out of an overall 52 individuals (some individuals weren't included because nearest-neighbor wasn't collared/identified) (Baden et al., 2020).

Data Analysis

Dyadic associations

For the purposes of this study, we defined dyadic associations as any time a nearest-neighbor was seen to be in the closest proximity to the focal animal followed. We counted all dyadic associations per 6 behavior types. Our final data set included a total of 48,171 dyads observed in 53,298 scans comprising a total of 40 individuals that included 13 adult females, 12 adult males, 8 juvenile females and 8 juvenile males.

We used a graph visualization software (Graphviz), which through use of a coding language, allowed us to create network diagrams of the animals summarizing their connections to each other for each behavior such that all dyadic relationships were illustrated by lines (vertices) that connected nodes (individual animals) in each behavior network. Relative thickness of the lines indicated the strength of the dyadic association. We ultimately presented the analysis of the behaviors vis-à-vis six (6) separate networks depicting individuals and their dyadic associations for each behavior.

Once we created all behavioral networks for all behavior types, we then compared them. The question we explored was whether network structure differed across behavioral categories. For example, does an individual tend to rest in the proximity of one associate (nearest-neighbor), but feed with another?

To illustrate how we did this, **Figure 3** shows a magnified section of both the rest behavioral network (left) and the feed/forage behavioral network (right). We wanted to see if animals stayed together from one network to the next; as well as if there were similarities between the two networks.

This figure highlights yellow, red, green and blue dyads that stay together from one network to the next; thus, all but one animal in rest is also seen in feed/forage. In looking at the structure of the networks, we note AM6 (yellow node) has 3 vertices (connections) in rest and 2 vertices in feed/forage; JM7 (red node) has 4 vertices in rest and 3 vertices in feed/forage; and so on. This difference in number of vertices per node in the networks accounted for the difference in the networks' appearance. In this snapshot example, rest has more connections than feed/forage making both networks look dissimilar- rest being denser (more vertices) than feed/forage, for example.
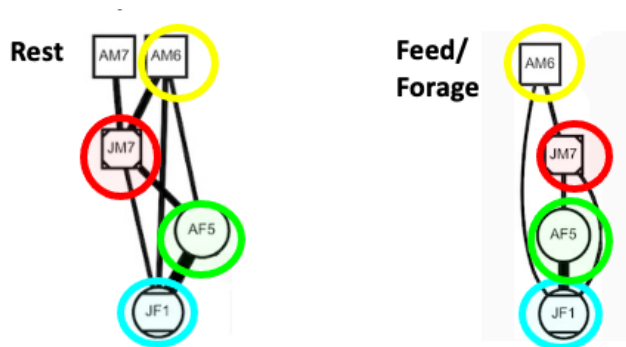

Figure 3. Network graphs comparing nearest-neighbors across behaviors. Magnified section of rest (left) and feed/forage network (right) shows dyads repeating in both networks except for one individual in rest (AM7). Vertices in rest appear thicker than in feed/forage.

We then created a complete behavioral network from the overall data for each of the six behaviors. From the plotting of these network associations, we were able to identify social preferences that we suspect are at play given the strength present in a particular network. The degree to which the network was large yet compressed (few color blocks) indicated to us that the network was indeed strong and cohesive (**Fig. 4).** If a network was small, we had to compare it to the larger, more robust networks to be able to discern if this network of animals was random or in fact intentional. We used the most robust network of rest as a model for this comparison. We additionally used a histogram to assist in further identifying which networks were the strongest, that is, which had the most dyadic representation. We also calculated the average number of nearest-neighbor present per focal animal, per behavior type. From this we were able to differentiate on average the frequency with which a focal animal had a new nearest-neighbor.

A.
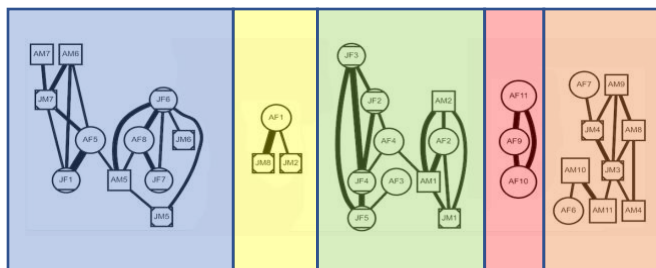
B.
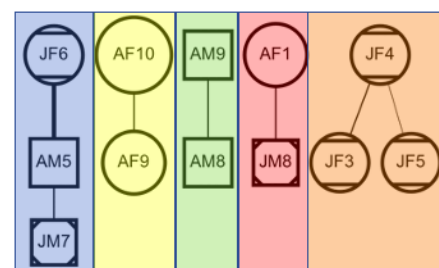
Figure 4. A. network graph of the behavior rest is composed of compact subgroups and thick vertices. B. network graph of the behavior play is sparse (thin vertices), making it difficult to assess its structure.

RESULTS

Behavior Networks

Common Behavior Networks

Of the six behaviors analyzed, we observed that two non-social behaviors were highly abundant (**Fig. 5**): rest (34.89 observations per hour) and feed/forage (18.97 observations per hour). Another non-social behavior, travel, was somewhat abundant (5.01 observations per hour). The three remaining social behaviors, mutual grooming, play and aggression, were comparatively rare (1.03, 0.08, and 0.03 per hour, respectively).

Figure 5: Histogram of hourly occurrence rate for each behavioral type. Rates were computed by counting the overall number of observations for each behavior and dividing by the number of observation hours.

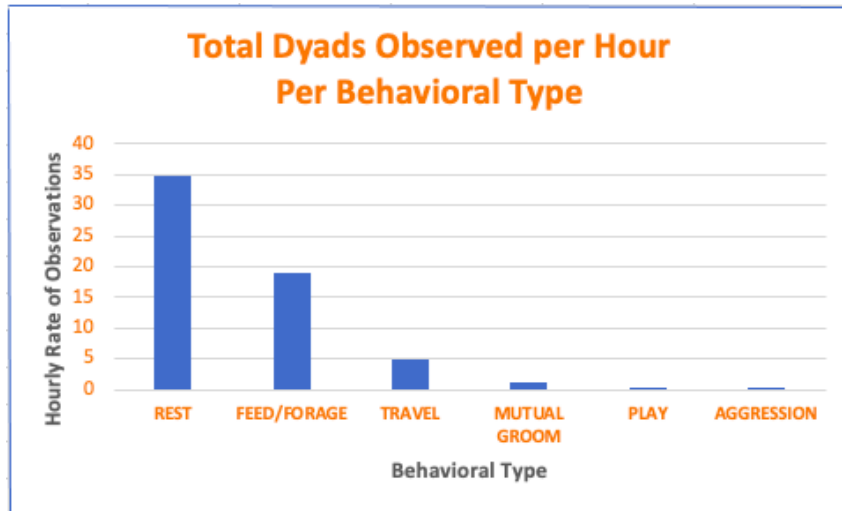Shown in **Figure 6** is a network that illustrates the association between a focal animal performing a specific behavior, and its nearest-neighbor animals during these behavioral events. The network summarizes the focal and nearest neighbor connections that are associated with each of the six behaviors. Each network is represented by nodes, lines, and colors. Each node denotes an individual animal, and the shape of the node signifies its sex and age such that female nodes are circular, male nodes are square, and delineated nodes represent juveniles. Nodes are connected to other nodes by lines (vertices). Each vertex indicates a dyad of a focal animal performing a behavior, and its nearest-neighbor animal during that behavior. The thickness ( ) of each vertex symbolizes the frequency in which the two animals (dyads) were observed as focal and nearest-neighbor during that behavior. Finally, each color block represents a connected group of animals (or subgroup) within the behavioral network. That is, nodes (animals) of the same colors are either directly or indirectly inter-connected by vertices.

Starting with the most abundant behavior, we see that rest has a total of 28,010 observations comprising 47 unique dyadic associations (**Fig 6).**
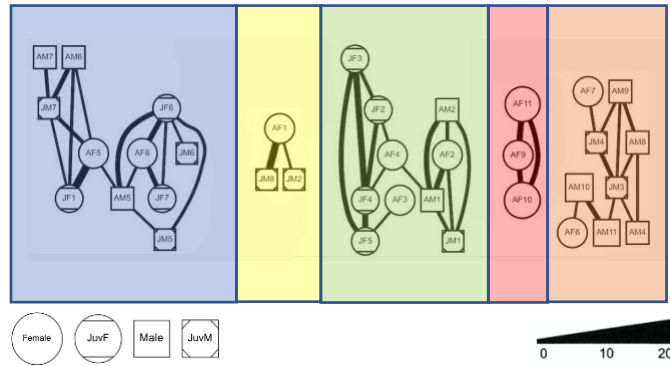
Figure 6. Network graph of rest behavior. This network shows the association between focal animals and their nearest-neighbors during rest. Line thickness represents the number of observations and rest represents the most cohesive and robust behavior network overall (average nearest-neighbor per focal 2.6).

What is immediately obvious are the thick vertices connecting the nodes in nearly each of the five, distinct subgroups. The average number of nearest-neighbor present with a focal (**Fig 7.**) for rest is 2.6 which is particularly low given the total number of observations seen (28,010).

Figure 7. Average number of unique nearest-neighbors per node (focal animal) for different behaviors, over the entire observation period of the study. This shows average number of

nearest-neighbor connections per focal in each of the six behavior types. The small numbers indcate the animals are highly conservative in their associations with others, despite being part of a fission-fusion community.

In contrast to rest, the feed/forage network in **Figure 8**, includes 38 distinct dyads which encompass a total of 15,227 observations. While the dyadic connections are still q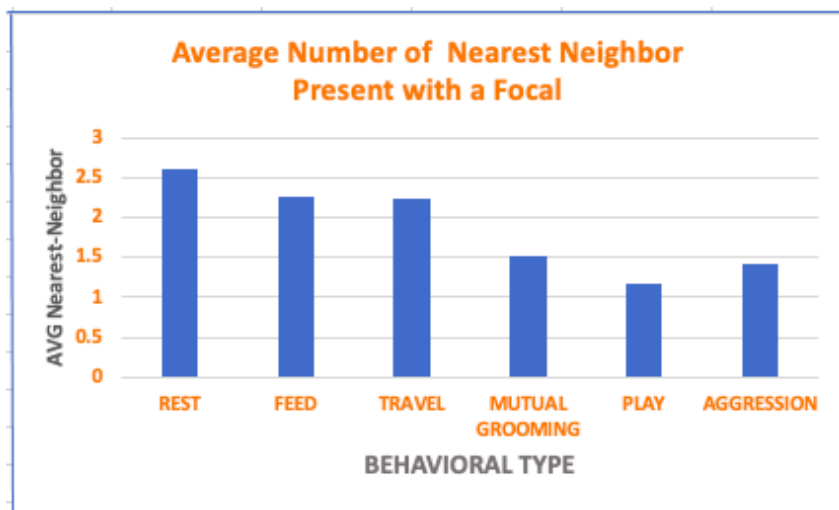uite strong as evidenced by the thickness of the vertices connecting nodes (average number of nearest-neighbor present with a focal is 2.2), this network has more subgroups (9) which suggests less cohesion and a higher fission-fusion dynamic present than was seen in the rest network.
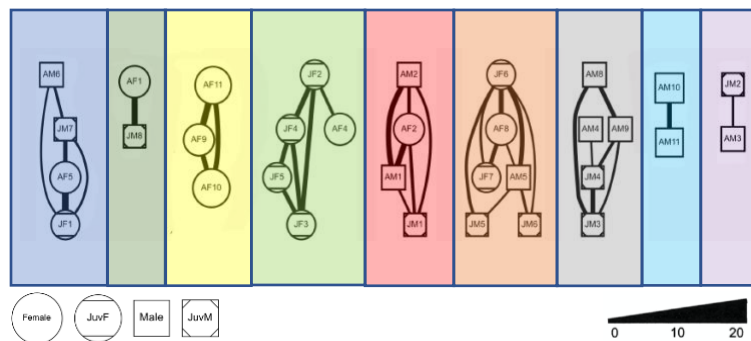
Figure 8. Network graph of feed/forage behavior. This network reflects persistent thick vertices denoting 2.2 average nearest-neighbor per focal in an expanded network configuration (9 subgroups).

Travel represents the last of the three non-social behaviors and is perhaps the least abundant behavior network of those previously described. This network (**Fig. 9**) contains 40 unique dyadic associations consisting of 4,020 nearest-neighbor observations of the behavior being performed. While this network has 40 connections, one can immediately observe thinner vertices herein as compared with the other two

networks. This is the result of fewer observations seen as evidenced by average number of nearest-neighbor present with a focal at 2.2. This network has 7 subgroups.
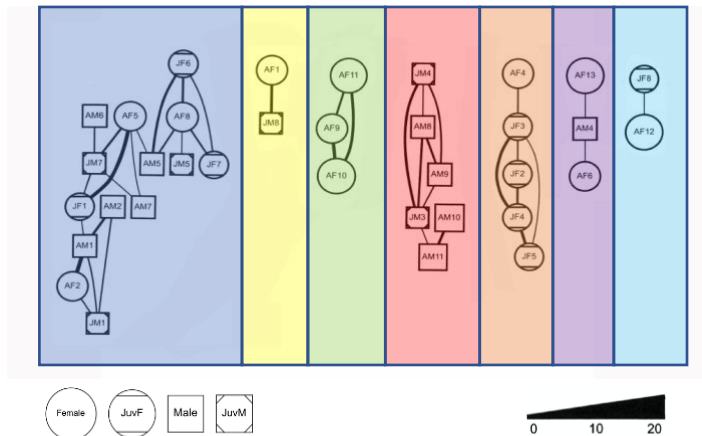
Figure 9. Network graph of travel behavior. We immediately see thinner vertices of all three common behaviors (2.2 average nearest-neighbor per focal) across the 7 subgroups in this least abundant network of the common behaviors.

Despite overall repeated dyadic partners observed across all three behavior networks (as evidenced by thick lines), very few *new* nearest-neighbors were involved in rest and feed/forage as compared with the network of travel which was the least abundant network of the three. It is the same individuals having repeated associations over a period of 24+ months of data collection (**Fig. 7**).

To provide additional perspective to the pattern of cohesion observed across all three networks, in **Figure 10** we trace 3 pairs of dyadic associates that stay together in rest, feed/forage and travel. Adult female AF11 in rest is observed as being strongly connected to adult female AF9 and we observe this dyadic association repeat itself in both feed/forage and travel. This pattern is consistent with adult males AM11 and AM10 in rest, as well as with adult female AF5 and juvenile female JF1, also in rest.

These same strong connections carry through to the feed/forage and travel networks indicating that the overall cohesive structure present in all three networks is similar to each other; the animals seem to be choosing to stay together across behaviors. As well, while we see similarity in structure across all three networks, we see more frequency in subgroups present in the feed/forage (9) and travel (7) networks than in rest (5), despite the fact that the animals are eating and traveling with the same groups of cohorts. This possibly highlights the high fission fusion dynamic of this ruffed lemur community.

10a. Rest Behavior Network Graph

10b. Feed/Forage Behavior Network Graph

10c. Travel Behavior Network Graph
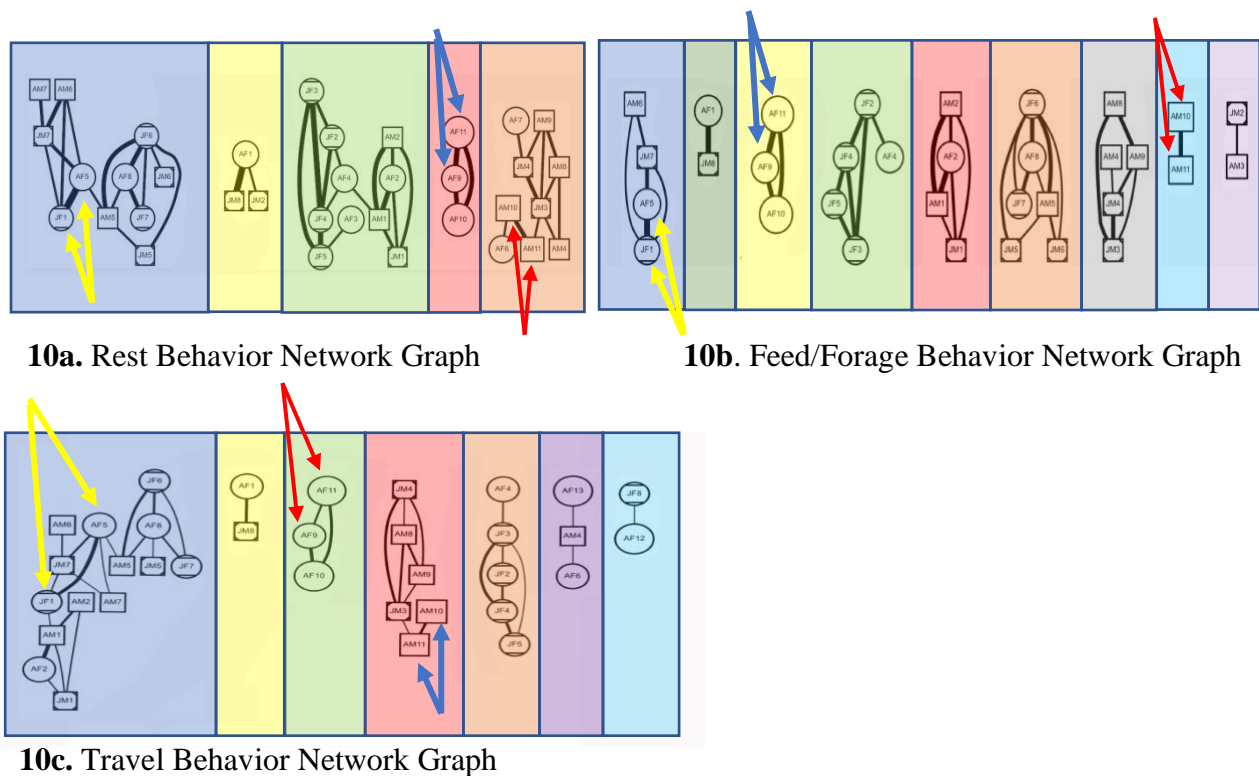
Figure 10. Three pairs of dyadic associates in rest that repeat in feed/forage and travel: Yellow = AF5 + JF1; Red = AF11 + AF9; Blue = AM10 + AM11

Rare Behavior Networks

The less abundant behavior networks of the six we analyzed are the three social behaviors of mutual grooming, play and aggression. Each network had small sample sizes: mutual grooming (0.3 observations per minute), but play and aggression had even smaller networks - play (0.02 observations per minute), and aggression (0.008 observations per minute).

In **Figure 11**, we see the largest of the rare behavior networks - mutual grooming – which includes 16 dyadic connections constituting 828 observations of the mutual grooming behavior being practiced. Vertices in this network are visually thinner than in others previously observed and because the network is sparse we're unable to determine if the 7 subgroups are distinct or random.
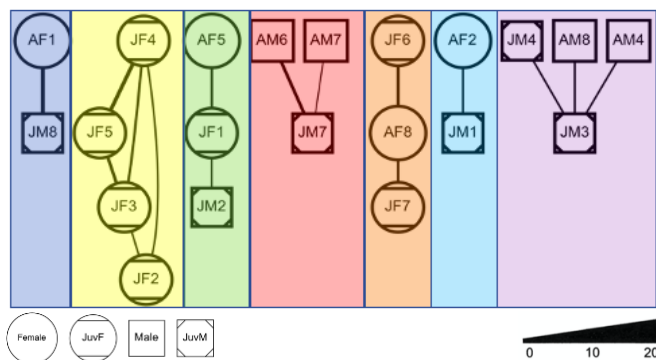
Figure 11. Network graph of mutual grooming behavior. The largest of the rare behavior networks incorporating 828 observiations of the behavior happening across 7 subgroups..

The final two behaviors of the six we've analysed include play and aggression and represent the smallest of all six behavior networks. The graph of the play network

(**Fig. 12**) shows 7 dyadic connections with 64 observations of the behavior. While this network is very sparse, there are five subgroups.
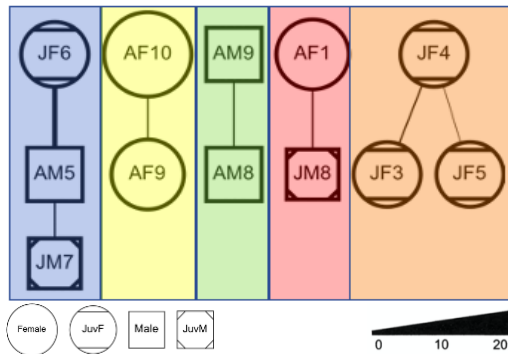
Figure 12. Network graph of play behavior. Average nearest-neighbor per focal is 1.1 as evidenced by this very small behavior network comprising a total of 64 observations of the behavior.

Finally, in **Figure 13** the graph of the aggression network maintains 10 dyadic associates across 4 subgroups. There are 22 observations of the behaivor occuring.
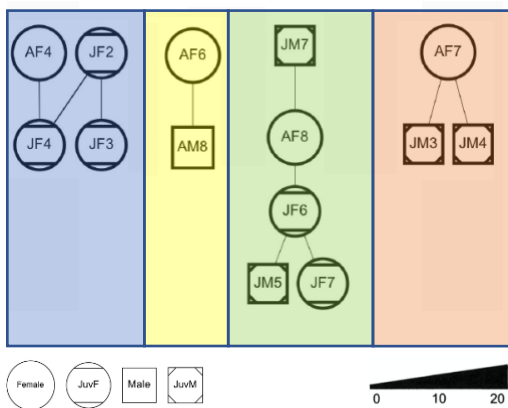
Figure 13. Network graph of aggression behavior. Very thin vertices are seen representing a 1.4 average nearest-neighbor per focal in 22 observations of aggression occuring.

In an effort to determine whether these three social behavior networks are consistent, despite their very reduced size, and that the dyadic associations present are also in the common, non-social behaviors, we used the rest network as a model to substantiate this as it represents the largest and most robust network overall. However, first we compared the non-social behavior networks to determine whether there was consistency across those networks. To do so, we incorporated a color overlay of the rest network and a gray version of the travel network (**Fig. 14**) and transferred the color from the rest network onto the corresponding nodes (animals) in travel.
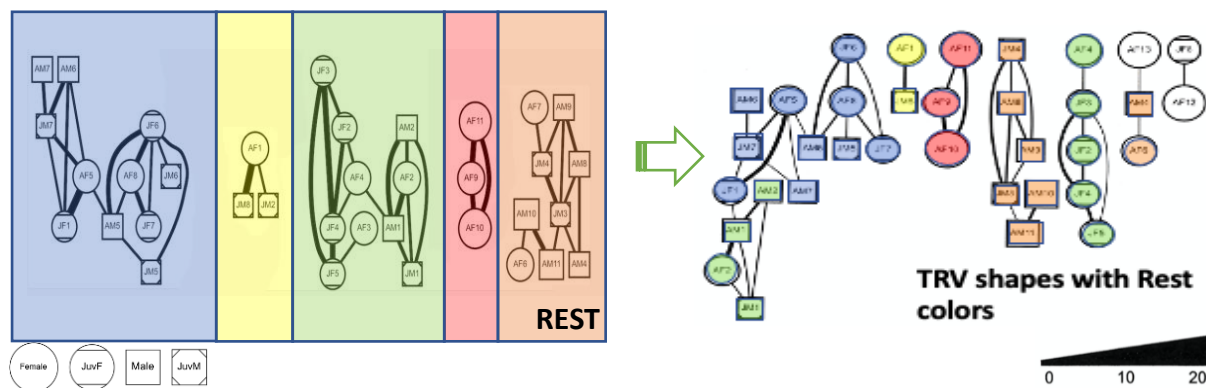
Figure 14. Travel compared to rest. Colors from nodes in the rest network are colored onto the corresponding nodes (individuals) in travel to show repeating individuals across both networks.

This showed distinct and consistent networks of individuals remaining in dyadic connections across the two behaviors. As well, two subgroups in rest (the green and orange subgroups) have split into two in travel: half of the large green subgroup has merged with the blue subgroup while the other half remains as a separate subgroup, and the orange subgroup has split into two. These splitting-fusing characteristics illustrate the fission-fusion dynamics occurring from one behavior network to the next.

Additionally, four juvenile females in rest's green subgroup (JF2, 3, 4, 5) remain connected in travel. Finally, any nodes left uncolored, such as the three gray nodes on the upper righthand portion of the travel network, represent those individuals in travel that aren't in rest, so the nodes remain gray.

In **figure 15** we evaluate feed/forage to the rest and travel behavior networks. In doing so we notice that the feed/forage network is made up of 9 subgroups as compared to rest's 5 and yet is similar to the network structure of travel's 7 subgroups. There is a split in the blue and orange subgroups from rest as well as the blue and red subgroups from travel, in feed/forage (fission-fusion) but overall, this network is revealing dyads that are staying together across all three of the non-social behavior types.
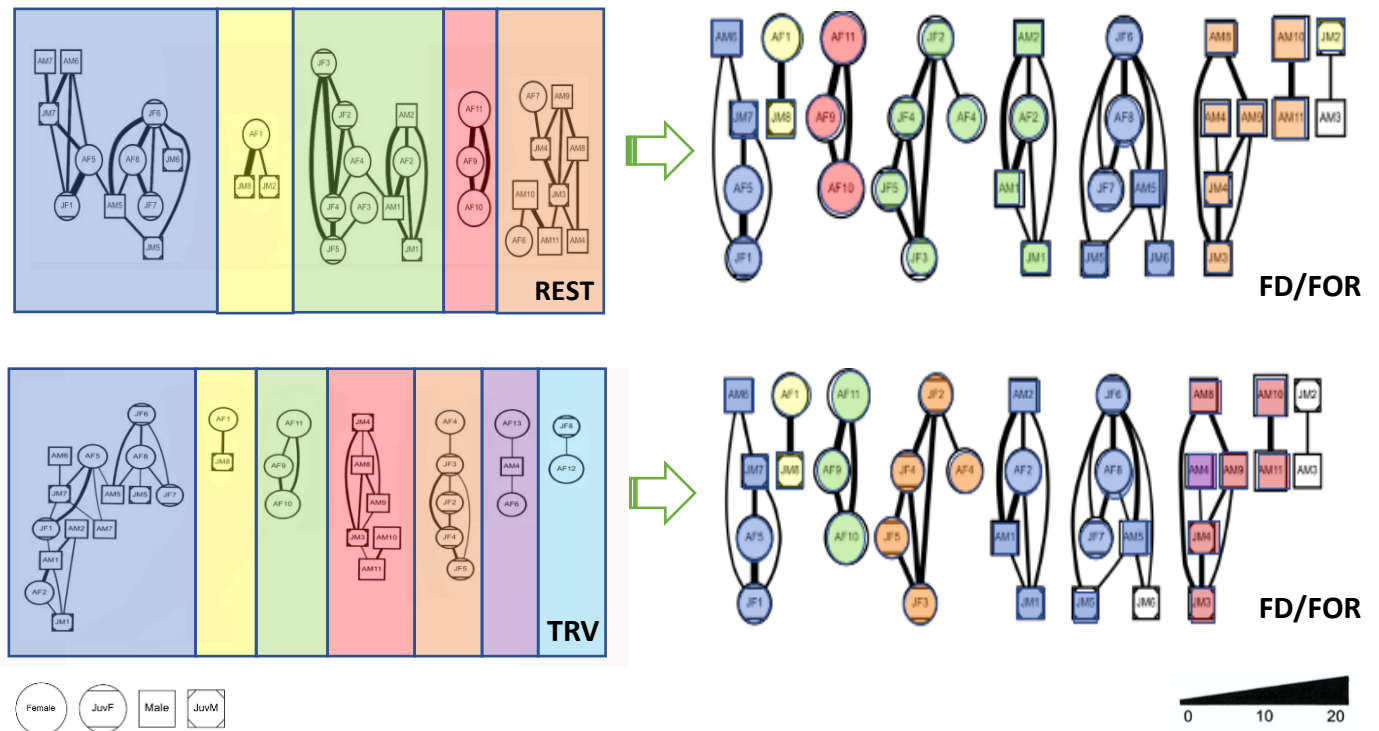
Figure 15. The feed/forage behavior network graphs with color overlay on the right assessed against the rest (upper-left) and travel (bottom-left) behavior networks show associates remaining together from rest and travel to feed/forage.

To assess whether the social behavior networks of mutual grooming, play and aggression represent strong, stable networks despite their reduced sample size and thus are generated from the more robust networks of the non-social behaviors in the previous section, we employed the same color overly technique to a gray rendering of the mutual grooming network in **Figure 16** and transferred the colors from the rest network onto the corresponding nodes in mutual grooming.

Here we see the blue, green and yellow subgroups in rest split into 3, 2 and 2 distinct subgroups respectively in mutual grooming which contains 7 subgroups overall as compared with rest's 5. While the incidence of observations documents an

extremely dramatic decline from rest (28,010) to mutual grooming (828), the color

overlay confirms that the mutual grooming network maintains a strong and stable

network of animals consistent with the large non-social behavioral networks.
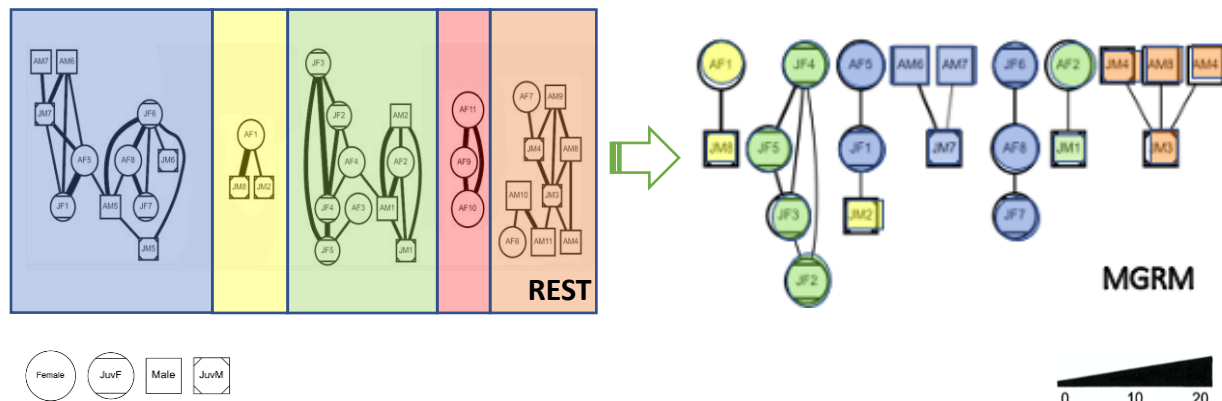
Figure 16. The network of mutual grooming with color overlay from the rest network on the left demonstrates that the rare behavior network of mutual grooming is a strong network and not random; animals are choosing to remain together across networks.

Assessing the smallest networks of the social behaviors of play and aggression

(rare behaviors) to the non-social behavior network of rest in **Figure 17,** we note similar

subgroup size in the rare behaviors (5 and 4 respectively) as compared to rest's 5.   It

is interesting to note that play contains a network of 12 individuals, of which half are

juveniles with 7 dyads observed. Aggression has 10 dyads of the 14 animals observed;

9 of which are also juveniles. Both behavior types display consistency with the rest

network despite their greatly reduced sample size.

Figure 17. The behavior network graphs of play (upper-right) and aggression (lower-right) with color overlay assessed against the rest behavior network on the left confirms that both smaller networks of the rare behaviors- play and aggression are also consistent with the common behaviors.

Evaluating both play and aggression against the mutual grooming network (**Fig. 18**) reveals a different outcome. Looking at play first, we see 3 subgroups transferring over from mutual grooming with 4 of the 12 nodes in play remaining gray. Aggression has 4 gray nodes out of 14 overall representing 4 subgroups from mutual grooming. It is interesting to note that fission-fusion dynamics are present even though both networks are very small: play has 12 members and aggression has 14. For the first time, consistency and degree of cohesion is shown not to be as strong across networks here; though the color overlay of mutual grooming against aggression shows more consistency. Two different trios of juvenile females from mutual grooming are observed

together in play as well as in aggression. But perhaps the most significant observation

that all three networks share is the small sample size and number of dyadic

associations in each.

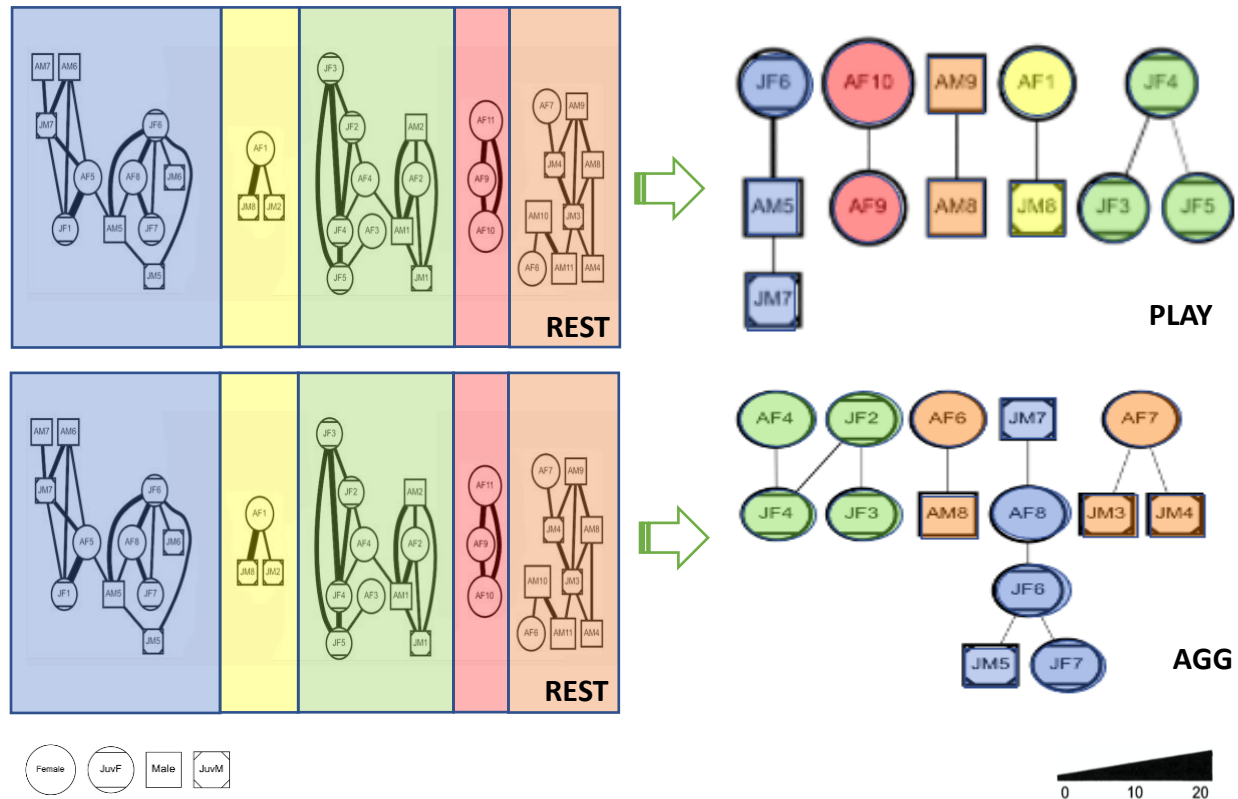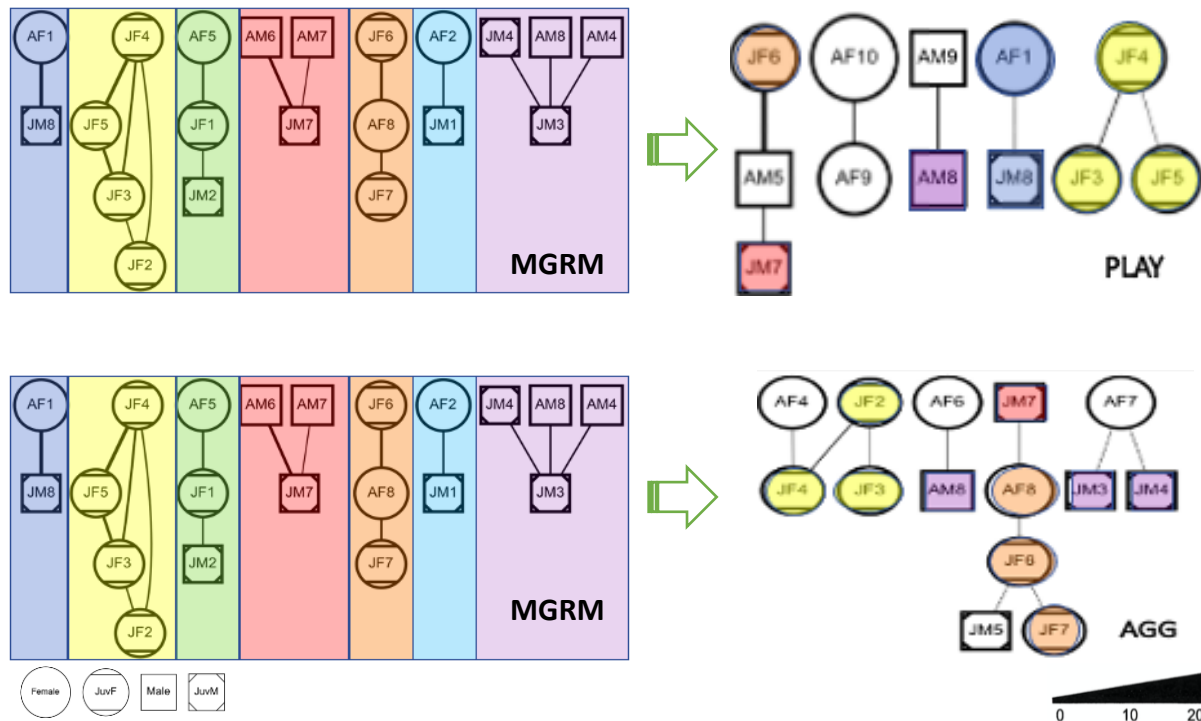**Figure 18.** The behavior network graphs of play (upper-right) and aggression (lower-right) with color overlay assessed against the mutual grooming behavior network on the left. The first time we see inconsistency across networks.

Lastly, we relate the smallest two behavior networks – play and aggression - against each other (**Fig. 19**). Although these two networks are consistent with the bigger networks of the more common, non-social behaviors, they aren't consistent with each other. The networks have very little overlap between them. For example, of the 14 animals in aggression we only see 5 that are colored from play. This underscores not so much that the networks are different but that aggressive individuals oftentimes aren't very playful. Also, there is a gap in connection in subgroups transferred from play to

aggression: the orange and blue individuals in the aggression network are each separated by a non-colored individual. We note this occurrence only in the evaluation of these two social behavior networks. Furthermore, the size of these networks demonstrates the low incidence of these behaviors happening at all when considering these counts make up 24+ months of data observation of these animals.
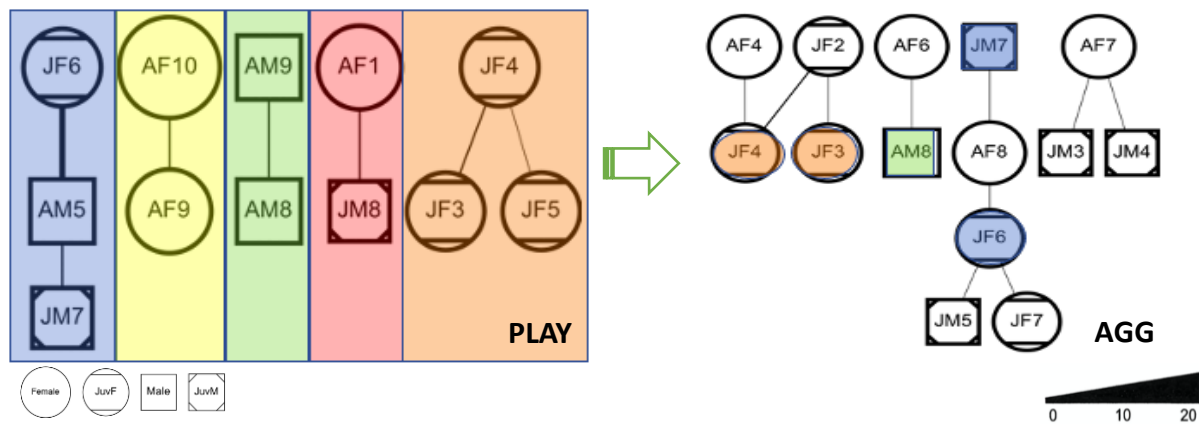
Figure 19. The behavior network graphs of aggression on the right with color overlay from the play network on the left highlights the small number of individuals from play colored in aggression (5 out of 14); and the orange and blue subgroups in aggression are broken up by an individual.

Overall, our data illustrate that although the social behavior networks are small in contrast to the larger, more robust networks of the non-social behaviors, we observe consistently stable dyadic connections.

DISCUSSION

My investigation provides support that although ruffed lemurs live in societies with high fission-fusion dynamics, when they are social, they do exhibit strong social preferences across the six behavior types analyzed of rest, feed/forage, travel, mutual groom, play and aggression. Additionally, while the network of rest had five subgroups, feed/forage had nine and travel had seven. This could be an example of the high fission fusion dynamic of this ruffed lemur community. Further, this analysis highlights that while the social behaviors of mutual groom, play and aggression are rare, their networks aren't random and are in fact formed from those of the larger, more common behavior networks. This would therefore seem to suggest that the animals are conservative about their choices and choosing to stay with specific individuals across all of the six behavioral types analyzed, and thereby exhibiting social preferences that do not appear to vary across behaviors practiced throughout the day. Note however, that we do not know who is being conservative: the focal (resting) animal, or the nearest-neighbor (who may be either resting or not).

This study also confirms the fact that ruffed lemur are not an inordinately social species – observations of mutual grooming, play and aggression were deficient (well under 100 observations in play and aggression over a 24-month period); yet these animals showed clear social preferences as to who they were close with across both common and uncommon behaviors. As such, it appears that ruffed lemur are exhibiting social preferences as other more prosocial species do including dolphin, honeybees, crows, and chimpanzees, etc., (Connor et al. 2000; Wild et al. 2021; St. Clair et al. 2015; Shimada et al. 2014).

Using descriptive statistics, we found that the average number of nearest-neighbor present while a focal practiced a behavior (average number of vertices per node) varied minimally across the behavioral states; that is, the overall range was between 1 and 2.6 for the six behaviors. Considering the high frequency of observations of the common behaviors practiced (total rest observed = 28,000+; feed/forage = 15,000+, travel = 4,000+) and the fact that these data were collected over a 27month time-period, these numbers are quite small indicating that the animals are seen with same nearest-neighbor associates repeatedly. Not only does this suggest the animals care with whom they rest but they also seem to eat and travel with the same associates as well as evidenced by this lack of variation in nearest neighbor. This suggests to us that these animals are highly conservative with who they share space with, and we eventually see this pattern emerge across all six behaviors moving forward.

In contrast, the social behaviors of mutual groom, play and aggression were observed very rarely (total mutual groom observed = 800+; play = 64, aggression = 22). Thus, we would expect their average number of vertices per node to be low (1-1.5) as the observations were sparse. However, in comparing these rare behaviors to the larger, more consistent networks of the common behaviors, we were able to substantiate that the rare behavior networks were in fact a true reflection of a conservative choice made on behalf of the animals, and not accidental. While this is true, the size and structure of these networks highlights the very small amount of time this population of animals spend practicing social behaviors at all in comparison to the more common behaviors of rest, feed/forage, and travel. This seems to suggest that

these animals aren't very social (though this inconsistency may also be an artifact of small sampling size).

This finding highlights the selectivity of this community of lemur in terms of who they are consistently close with. Animals maintained nearly the same nearest-neighbor associates throughout the behaviors of rest, feed, travel, mutual groom, play and aggression despite being in what is considered a high fission-fusion community. We found that the preferences shown did not appear to vary across both common and rare behavioral states and this complements what is already known about these animals from Baden et al (2020).

To supplement this, we noted a group of juvenile females seen collectively throughout the networks of both the common and rare behaviors; albeit the number of individuals in the group varied from one behavior to the next (fission-fusion). These juvenile animals were likely pre-dispersal siblings that hadn't left their natal group yet and were therefore sticking together. The adults however were not showing this bias thus the networks in our study further validate that association of these animals is unrelated to kinship in adults (Baden et al 2020).

To address the difference in the thickness of vertices between nodes, we cite several explanations for this. One possibility is that an individual simply preferred to rest (or feed/forage or travel, etc.) with a particular associate more than with another associate. Another possible scenario is that there were more observations of that individual resting with a particular associate than with another.

It's important to note that in this analysis the networks don't reflect who is who in regard to focal and nearest neighbor and in fact most animals were observed in both

positions throughout the behaviors in the data, so symmetry was unaccounted for. In addition, in an effort not to skew what was seen, the data analyzed here represented the raw data of the six behavioral states. This was based on the supposition that only the behavior states themselves would change in terms of behavioral observations and that the sample sizes across behavioral types were exactly the same. Thus, no attempts at normalization of sample size of these data were included in my analysis.

LIMITATIONS

Our results provide some support that *V. variegata* do exhibit social preferences across behavior types. However, as our work represents the first baseline study in analyzing raw data counts using nearest-neighbor as an indicator of preference, we recommend future endeavors to employ the more widely accepted measurement of association indices to assess relationship strengths across behavior types. As we didn't concentrate on the specific relationships between associates themselves and focused only on the structure of the behavioral networks and whether animal associations were repeating themselves across the different behaviors, we didn't see this as a concern. However, it would be relevant to know how the results of association indices and raw number counts compare. We would expect that perhaps the social ties (vertices) between the animals might change (thinner; thicker) but that the actual networks themselves would remain largely the same.

FUTURE STUDY

As this study used nearest-neighbor as an indicator of social preference expressed among focal animals, we are unable to evaluate its efficacy against subgroup size as a proxy until we compute association indices for our focal and nearest-neighbor associates. This would seem to be a valuable exploration that may elucidate relationship between the focal and nearest-neighbor further.

CONSERVATION IMPLICATIONS

Approximately half of the Madagascar rainforest has been lost due to anthropogenic pressures consisting of habitat loss and degradation as well as illegal hunting for human consumption (Baden et al. 2019; Vieilledent et al. 2018). Deforestation due to human population expansion and slash and burn agriculture continue at alarming rates, yielding open stretches of land surrounding leftover forest 'patches' that *v. variegata* can be averse to crossing (Morelli et al. 2020; Holmes et al. 2013). This can spark a domino effect that not only includes preference constraint, but, reproductive isolation, weakened genetic diversity and overall reduction in species fitness (Louis Jr et al. 2005). This, heightened by the effects of a warming planet, has the potential to further reduce appropriate habitat for the species by up to 90% in only 49 years (Morelli, et al. 2020).

One of the advantages to understanding the behavior decisions of individuals of a species is that we may be better able to predict their behavior choices in changed environments such as those that have been altered because of human-induced origin (Sutherland 1998). As such, examining the consequences of habit fragmentation &

loss, for example may be improved by including the use of such social preference paradigms. Of course, to justify such endeavors, studies would need to be achieved faster than habitats continue to alter. Since social structure may influence spatial patterns and density, ultimately impacting genetic diversity, knowing the possible impacts that habitat loss and degradation can have on a species' social preferences may help mitigate long lasting deleterious effects on overall fitness (Wilson 1975).

The impact of species' behavior on conservation direction and efforts can't be emphasized enough. The significance of social structure in regard to conservation efforts was underscored in a 2015 study by Parreira et al., which demonstrated that sociality indeed maximizes genotypic diversity; thereby contradicting the misconception that social groups can be subject to genetic drift and increased incidence of inbreeding.

Additionally, knowledge of social preferences has the potential to greatly improve the welfare and management of captive groups of various species. For example, social network analysis has been used to study the effects of relocation on stress & use of space (proximity) in captive groups of capuchin monkeys as well as in squirrel monkeys (Dufour et al. 2011). Beisner et al (2011) used social network analysis to establish the degree of integration required when incorporating a group of high-ranking natal adult males into an existing social network group of rhesus macaques.

Moreover, social network analysis can be used to evaluate general procedures used in zoo settings, as has been done for captive Rothschild's giraffe (Lewton et al. 2020). This gave insight into the flexibility the animals were demonstrating in choosing associates, which resulted in subsequent suggestions to zoo staff that herds managed

should include a range of individuals from which animals may choose a desired

associate from.

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