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Social networks differ depending on aggressive and affiliative interactions of captive ring-tailed lemurs (*Lemur catta*)

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Abstract

Social network analysis provides a deeper understanding of the dynamic social relationships within a social group through identifying centrality, subgroups, isolated individuals and preferred or avoided dyads which have shown effective for the study of dominance hierarchies (Funkhouser et al., 2018). However, this is rarely used in captive environments despite showing promise for its management. In this study, social network analysis was used to investigate the dominance hierarchy, dyadic and group-level social relationships in a captive group of 11 ring-tailed lemurs (*Lemur catta*) at Bristol Zoo Gardens. Focal-animal and instantaneous scan sampling were used to collect 90 total hours of associative, aggressive and allogrooming interactions from October to November 2018. Data was analysed using R to compute social networks and centralities. In Minitab and SPSS, correlations and chi-squared tests were conducted to detect differences in male scent marking, aggressive and grooming behaviours. Results matched previous studies with female dominance, linear hierarchies and dominant males scent marking more frequently. Aggression increased with food and individuals exhibited few extreme aggressive behaviours. Agonistic networks had a higher variability of centralities compared to affiliative networks which had a more even distribution of interactions. More dominant individuals were generally more central, initiated more aggression and received more grooming. Finally, the bigger the difference in dominance, the more cautious subordinate individual behaved across all networks. Results indicate that all individuals act to increase their own social benefits. They also highlighted which individuals are important for group cohesion and the different approaches individuals use based on their position within the group. The information found can be used to help manage this group to ensure the improvement of group welfare, supporting growing evidence that social network analysis is invaluable for captive applications aided further when combined with classic data analysis.

Introduction

Sociality implies a group of individuals that live and or interact together which can lead to complex social structures and bonds (Whitehead, 2008). These bonds have an adaptive value across taxa (Silk, 2007; Majolo et al., 2012; Vanthournout et al., 2016) as social structure creates selective pressures on the group affecting individual health, fitness and welfare (Rose & Croft, 2015). The specific effects of selective pressures depend on the social structure and individual rank (Majolo et al., 2012). Previous research has discovered diverse social systems maintained by differing social factors. However, these studies are limited as they focus on the dyadic relationships of two individuals (Silk, 1999; Arnold & Barton, 2001), whereas the relationships studied often extend beyond this pairing to the group level (Farine & Whitehead, 2015).

Social network analysis (SNA) has emerged as a promising tool to assess social structure across species at all social levels and for all types of interaction (Couzin & Krause, 2003; Krause et al., 2007; Farine & Whitehead, 2015). Although it has been around for decades (Biggs et al., 1986) SNA has only recently become popular due to technological advances (Strogatz, 2001) being increasingly applied to explain the social structure and function of a range of taxa (Corner et al., 2003; Lusseau, 2003; Croft et al., 2005; Flack et al., 2006). SNA provides a deeper understanding of the behaviour of individuals at the group level (Couzin & Krause, 2003) and is achieved by looking at interactions between all group members to identify and quantify social relationships not captured by more common measures (Krause et al., 2007; Wey et al., 2008; Sih et al., 2009; Hirschi., 2010). It can also identify clusters, subgroups, isolated individuals and preferred or avoided dyads (Funkhouser et al., 2018). Centrality is one method commonly used, although there are several types, they all generally calculate each individual's importance within the social group: the higher the centrality, the larger individuals influence on the group (Farine and Whitehead, 2015). As a result, SNA has revealed that social structure can be determined and maintained by differing factors such as dominance, affiliation, age, sex, aggression and relatedness (Sueur et al., 2011; Makagon et al., 2012; Pinter-Wollman et al., 2013; Farine & Whitehead, 2015). However, social structure is commonly caused by a combination of these factors with their exact influence being species or even population specific (Chapman & Rothman, 2009).

Primates show some of the most complex social systems each influenced differently by the factors listed previously, thus their social structures are often oversimplified by existing classification methods (Sueur et al., 2011). Primates have been studied using SNA for much longer than other classes allowing for a more comprehensive understanding of their social structure (Brent et al., 2011). For example, SNA has highlighted that despite being closely related, Rhesus macaques (*Macaca mulatta*) choose to associate with higher ranking or related individuals, whereas Tonkean macaques (*Macaca tonkeana*) have the same likelihood of associating with any individual (Sueur & Petit, 2008). This demonstrates that SNA has proved invaluable in defining and illustrating the diversity of primate social structures and the factors which determine them, by providing a much finer picture of their internal structure (Kasper & Voelkl, 2009).

Ring-tailed lemurs (*Lemur catta*) are a primate species with a rare social structure, female dominance, which has been seen to some extent in all lemur (*Lemuroidea*) species (Hemerijk et al., 2008). Female dominance is thought to be an adaptation to the high cost of reproduction and lack of resources compared to other primates (Pereira & Kappeler, 1997). The lack of resources is caused by their environmental location, with lemurs being endemic to Madagascar resources are harder to come by as islands have a temporally and spatially variable environment (Frankham, 2008). Female dominance overcomes this by giving females priority access to resources vital for successful reproduction. This unusual social structuring makes this an interesting species to apply SNA to. To date, there are a handful of SNA studies published for this species. These have included research on how individual knowledge influences centrality (Kendal et al., 2010), how centrality changes with differing personalities (Kulahci et al., 2018) and how forest fragmentation affects social structure (Bodin & Norberg, 2006), however, this research is specialised.

Fundamental aspects of ring-tail lemur social structuring have been researched via traditional methods, which have discovered that wild ring-tailed lemurs live in equal sex ratios averaging at 10-20 individuals per group. They have matrilineal dominance hierarchies with alpha females retaining dominance for around five years (Wilson & Hanlon, 2010). Although females are dominant over males, linear dominance hierarchies occur within each sex (Gould, 1996b), where typically the alpha male has priority access to females and food (Sauther et al., 1999). Furthermore, males rarely show aggression as this can decrease attractiveness, so instead use alternative methods such as scent marking to settle disputes (Kaburu & Newton-Fisher, 2015). Social structure is maintained firstly by affiliative behaviours via touching and grooming (Gould, 1996a), mutual affiliative interactions occur more between closely related individuals and matrilineal lineages (Taylor & Sussman, 1985). Whereas unidirectional affiliative behaviours are initiated more commonly by subordinate individuals (Nakamichi & Koyama, 1997), who direct grooming on areas inaccessible to dominant individuals to gain social benefits in return (Grueter et al., 2012). Secondly, agonistic interactions determine dominance, with dominant females being prime aggressors. Aggression is more frequently seen when defendable resources, like food, are present (Lu et al., 2008). Generally, aggressive interactions begin less extreme, however if they cannot be settled aggression will escalate to fighting or biting (Jolly et al., 2002). Submissive gestures, used by subordinates, indicate to dominant individuals they recognise their subordination to quickly resolve conflict and prevent injury (Hosey & Thompson, 1985; Wilson & Hanlon, 2010).

However, due to threats such as hunting and deforestation ring-tailed lemurs are currently endangered so are housed in captivity for conservation (Andriaholinirina et al., 2014). Like many primates, they are usually held in environments lacking natural stimuli, so do not accurately mimic their native habitat preventing them from exhibiting their full range of behaviours (Hosey, 2005; Tarou et al., 2005). More recently, SNA is being considered as a practical application for captive management, this is important to pursue as complex social interactions essential for survival in the wild, such as vocalisations and body language, are not always encouraged in captivity so are lost (Benirschke, 1986). SNA has already been used to predict how group stability changes when individuals are removed from the group (Flack et al., 2006), or how disease spreads depending on their importance (Jacobs & Petit,

2011). Illustrating that this method shows promise for captive management (Rose & Croft et al., 2015).

Changes in captive ring-tailed lemur behaviour from wild behaviour have already been recorded, for example, wild ring-tailed lemurs adopt female philopatry, where females remain in their natal territory and males disperse, however captive males cannot do so creating an unequal sex ratio unless manually moved (Mertl-Millhollen, 2006). However, moving individuals between zoos can upset existing social bonds and hierarchies depending on their social importance (Flack et al., 2006). Also, mating pairs are manipulated to create the best genetic diversity, but individuals that are more aggressive towards keepers are less likely to be bred. However, these traits are suited to increasing survival and reproduction in the wild (Ryder, 1995). The social changes from being held in these abnormal social conditions may impact individual physiology and physical wellbeing (Hosey, 2005; Sandel et al., 2011), in addition to influencing the groups social network compared to their wild counterparts.

The aim of this study is to apply SNA combined with more classical data analysis to a group of captive ring-tailed lemurs. To help understand how agonistic and affiliative interactions vary between individuals depending on their dominance, relatedness, sex and the presence of food. It is hypothesised that females will be more dominant than males, with a linear hierarchy in both sexes. The presence of food is expected to increase agonistic interactions. More dominant individuals are expected to receive more grooming, initiate more aggression and have a higher association with all individuals with the opposite pattern for subordinates. Extreme aggressive behaviours are expected to be displayed when dispute cannot be settled. Individuals of a lower rank should groom more dominant individuals on inaccessible areas to gain the most social benefits. Finally, more dominant males are expected to scent mark more frequently. This information will help to provide a better understanding of this group whilst improving the knowledge of lemur social behaviour, both aiding future captive management.

Methodology

Ethical Note

Before any observations were conducted on the ring-tailed lemurs at Bristol Zoo Gardens, an animal Ethics Proposal and Off-Site Risk Assessment were submitted to the Plymouth University Animal Ethics Committee for approval. As this study only involved the observation of animals in their normal environment with no interactions or manipulations, no further ethical approval or considerations were required.

Study Subjects and Site

Study subjects consisted of 11 captive ring-tailed lemurs: three males, five females and three juveniles (Table 1). These were housed at Bristol Zoo Gardens in an enclosure containing an on-show and off-show indoor area, and an outdoor area which was a public walkthrough (Fig.1).

Table 1: Group composition information about each ring-tailed lemur involved in this observational study.

Name	Sex	Age Category	Age at time of study	Dam
Afu	Male	Adult	6 years 7 months	-
Muriel	Female	Adult	12 years 7 months	-
Mavis	Female	Adult	7 years 7 months	Muriel
Ethel	Female	Adult	7 years 7 months	Muriel
Leo	Female	Adult	3 years 3 months	Mavis
Dot	Female	Adult	2 years 7 months	Mavis
Alfa	Male	Subadult	1 years 7 months	Mavis
Darla	Male	Subadult	1 years 7 months	Ethel
Shirley	Female	Juvenile	7 months	Mavis
	Unknown at time of study			
Theodora (Twin)	Female	Juvenile	7 months	Ethel
	Unknown at time of study			
Nelly (Twin)	Female	Juvenile	7 months	Ethel
	Unknown at time of study			

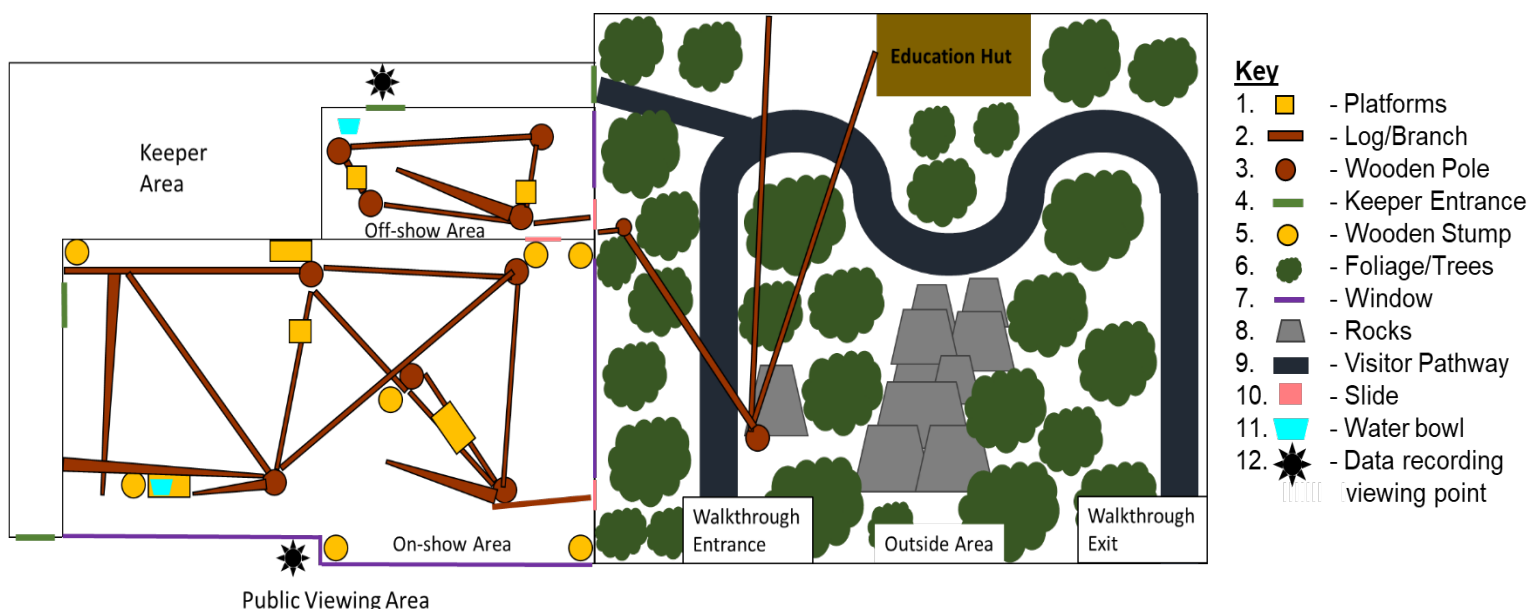


Figure 1: Birds-eye-view of the ring-tailed lemur enclosure at Bristol Zoo Gardens, not to scale.

Behaviour Sampling

An ethogram was created by adapting elements previously described by Pereira and Kappeler (1997), Waeber and Hemelrijk (2003) and Shire (2012) containing agonistic, submissive, grooming and play behaviours to avoid confusion with agonistic behaviours (Shire, 2012) (Table 2). Two individuals were classed as associating if they were within one meter of each other, this is smaller than the distance specified by Tiddi et al (2012) however, they observed wild primates therefore individuals were not limited by enclosure size which could cause association by chance.

Table 2: Description of behaviours used for collecting data

Behaviour	Code	Definition
Agonistic Behaviour		
Stink fight	SF	An individual rubs its tail with hands after rubbing their scent glands then directs and shakes its tail towards the target conspecific.
Cuff	CU	An individual reaches out hand and manually (or attempts to) hit target conspecific in an aggressive manor.
Fight	F	An individual attacks the target conspecific with arms, biting and for an extended period of time. Often followed by vocalisation.
Chase	CH	An individual runs towards and pursues an evading conspecific for more than 3 meters.
Displace	TP	An individual obviously runs towards a target conspecific and directly occupies the targets previous location.
Lunge	L	An individual moves upper torso towards a target conspecific without moving hindquarters, causing the target conspecific to retreat.
Bite	B	Individual uses its mouth to grab or cut a conspecifics body part in an aggressive manor.
Grab	G	An individual rapidly seizes a conspecifics body part or pelage in an aggressive manor with both arms.
Take Food	TF	An individual directly attempts to directly remove a food item from another's hands or mouth
Scent marking	SM	Individual rubs or holds glands found on genitalia, wrists and arms against a surface.
Submissive Behaviours		
Move Away	DI	An individual immediately runs away after looking at or participating in a non-play interaction with a conspecific to avoid them (>1.5m)
Cower	CO	An individual quickly lower their body or pulls a body part away from another conspecific (<1.5m).
Submit Food	SF	An individual gives up a food item they are in possession of in response to an agonistic attempt from a conspecific to take the food
No Reaction	NR	An individual shows no behaviours in response to an attempt of an agonistic interaction from a conspecific

Affiliative

Behaviours

Mutual groom	MG	An individual and conspecific both use the grooming claw or teeth to clean each other simultaneously or in close alternation.
One-way groom	OG	An individual grooms a recipient conspecific using the grooming claw or teeth to clean, without the grooming being returned.
Sit near	SN	An individual sits within 1 meter of another conspecific.
Sit in	SC	An individual sits while touching another conspecific, excluding tails.
Contact		
Mate with	M	Copulation occurs between two individuals

Play

Behaviours

Play	PW	Two individuals compete to hold onto their conspecifics pelage with their hand, feet or mouth. No agonistic behaviours or vocalisations occur.
Wrestle		
Play chase	PC	Where individuals will try to overtake each other in a relaxed manor, changing roles. No agonistic signals or vocalisations occur.
Out of Site	X	Animal is not visible
Other	OT	Other behaviours which appear to be agonistic or affiliative not mentioned above.

Observation Methods

Six pilot studies occurred in August and September to: Identify individuals, create an ethogram, edit data collection methods and practice the final data collection procedure. Data collection occurred during daylight hours between 8:00am and 4:30pm on 20 randomly selected days between October 2018 and November 2018, where each lemur was observed for a total of 13 hours. Data was collected from two parts of the enclosure (Fig.1): the public area, and off-show keeper area, my presence would not influence lemur behaviours as they had already habituated to the presence of people in these areas. Each day consisted of three 10-minute sessions, one during each of the three feeds where all individuals were observed via scan sampling, and eight 30-minute focal samples when not feeding. Within each 30-minute sample, six individuals were observed consecutively for five minutes each, resulting in each individual being observed via focal sampling four times each day. The order of focal observations was selected randomly to eliminate bias (Shire, 2012; Tididi et al., 2012; Waeber & Hemelrijk, 2003).

Recording of feeding sessions began after the keeper left the enclosure after providing food, ensuring their presence did not affect lemur behaviour. Behaviours influenced by food or enrichment stopped after 10-15 minutes when the whole group lost interest in food - indicated by no interaction with food or enrichment, resting, or moving away. Therefore, a period of 30 minutes would be left after these were added before recording any non-feeding sessions, to ensure they did not influence the behaviours recorded. When training occurred, data collection stopped until training had ended. Although food was generally present throughout the whole day, no agonistic behaviours occurred outside of feeding sessions, suggesting there was no competition for food during these times.

For both feeding and non-feeding sessions five behaviours were observed. Two state behaviours: location and association, and three event behaviours: aggression, allogrooming and male scent marking. Event behaviours were recorded via ad-libitum sampling of all individuals during all feeding and non-feeding sessions, totalling to 4.5 hours of observation each day. These were only recorded when all individuals were visible to eliminate bias. State behaviours were recorded via instantaneous sampling in one-minute intervals, for only the focal individual during non-feeding sessions and for all individuals during feeding sessions. A Dictaphone was used to verbally record data during feeding sessions, so no behaviours were missed (Altmann, 1974; Martin & Bateson, 2007). Although location was recorded, this was not analysed further.

Allogrooming

Allogrooming was recorded by the counts of occurrences rather than the length of the interaction (Waeber & Hemelrijk, 2003), due to the difficulty of recording all data. In each grooming occurrence the individual who initiated and received allogrooming was recorded, in addition to if the grooming was returned and who ended the allogrooming session (Hosey & Thompson, 1985; Nakamichi & Koymoa, 1997). The body was divided into two regions to record the location of where each individual groomed, as this can indicate dominance (Franz, 1999). Firstly, the face and head regions (upper half) and secondly, the back and anogenital regions (lower half).

Aggression

Aggression was recorded by counts of occurrences as most interactions were resolved in several seconds so were difficult to record accurately. In each occurrence, the identity of the individual initiating and receiving the aggressive interaction was recorded (Norscia & Palagi, 2015). For polyadic aggressive interactions (more than two individuals involved), only the initial aggressor and receiver were recorded due to the difficulty of determining other individual roles (Tiddi et al., 2012). In addition, the agonistic behaviour exhibited from both individuals was recorded and the winner. A winner would be decided when one individual would only exhibit submissive behaviours in response to the agonistic behaviours exhibited by their conspecific, indicating that both individuals recognised their dominance positions (Vervaecke et al., 2000).

Statistical Analysis

Data was entered into Excel then transferred into SPSS, Minitab and R v3.5.2 using the package 'igraph' for analysis. An average of all data collected for the twins was calculated as they could not be distinguished so were treated as one individual for analysis. The average of the twin counts sometimes produced decimals (0.5), for statistical tests which could not process data with decimals, all data was doubled.

The dominance hierarchy was determined by creating a weighted dominance index (DI) from agonistic interactions, which was achieved by creating a win/loss matrix and calculating the Dominance Index = $\#win/\#(win+lose)$ per pair-wise interaction. An average was then calculated for each individual ranging from 0-1, the higher the DI, the higher the individual's dominance (Waeber & Hemelrijk, 2003). Agonism was chosen because it is consistent with other behaviours in determining dominance in ring-tailed lemurs (Bauer, 2004). Individuals were grouped into three ranks for

feeding and non-feeding. To determine which individuals belonged in each rank, the range between the maximum and minimum possible value for a DI (0-1) was split into three equal ranges. Individuals with a DI within each range were assigned that rank, named: high ranking (DI = 0.67-1), medium ranking (DI = 0.34-0.66) and low ranking (0-0.33). It is argued that applying rank-order to non-human primates is an unconscious anthropomorphism (Rowell, 1974) with ring-tailed lemurs not recognising rank but only those dominant or subordinate relative to themselves (Bauer, 2004). However ranking individuals in this study was for illustrative purposes rather than attributing definitive ranks.

R

In *R*, four sociograms were created to illustrate SNA for aggression, association and affiliation. As food presence directly affects aggression, feeding and non-feeding data were both used for SNA, because food does not affect affiliative behaviours, these rarely occurred during feeding therefore only non-feeding data was used for SNA. Sociograms consist of nodes representing individuals and are connected by edges, lines representing the relationships between nodes. Directed sociograms have arrows on edges indicating the direction of the relationship. These were created for aggression and allogrooming using an edge list weighted by the number of occurrences of the directed behaviour for each pair. Undirected sociograms only illustrate the presence of a relationship, the was created for the association of individuals using an adjacent matrix weighted by the number of occurrences pairs spent associating.

Each sociogram was clustered into groups to illustrate community structures using the spin glass command based on Pott's Spin Glass Model (Wu, 1982). This produces a modularity value ranging from 0-1, the higher value, the more distinct the community structuring (Newman, 2004) where individuals in each community more commonly interact than those in different communities. Clustered communities in small networks are often over exaggerated, therefore this study did not assume these communities existed however, was useful to highlight data trends. Eigenvector centrality coefficient (ECC) determines an individual's influence on the group. The higher the ECC, the more social partners they have who also have many partners, increasing their influence in the group. This was calculated for aggression with and without food, allogrooming and association and plotted as sociograms.

SPSS

In *SPSS*, Spearman's Rank correlation coefficient was calculated to determine if there was a relationship between: receiving and ending grooming, initiating and receiving grooming, initiating and receiving grooming on the upper half of the body and the same for the lower half of the body. The previously determined dominance rank was used to indicate how the relationship of initiating and receiving grooming on the lower and upper-half of the body changed with rank, illustrated via directed sociograms.

MiniTab

A chi-squared goodness of fit test determined if the frequency of scent marking varied depending on the individual male, and a binomial test was used to determine if this also varied with food presence. The hypothesis test accounted for different proportions of time spent recording feeding and non-feeding sessions, testing against a p-value of 0.05. A chi-squared test for association was used to test for differences in the number of scent marks when looking at both individual males and whether food was present, in addition to any differences in the type of aggressive and submissive behaviours emitted depending on dominance rank. As multiple tests were carried out on the same data, Bonferroni corrections were calculated by dividing 0.05 by 30, the number of tests carried out on both feeding and non-feeding aggressive behaviours, to create the adjusted p-value which was 0.001. The critical chi-squared value was calculated to select which behaviours differed significantly from their expected values when looking at their contribution to chi-square.

Results

There were a total of 1087 aggressive interactions 11 of which had no clear winners so were omitted from the data. The number of aggressive interactions dropped by around half from 766 to 310 when comparing feeding to non-feeding sessions. 1354 of the total 1372 grooming occurring during non-feeding sessions.

Dominance Index

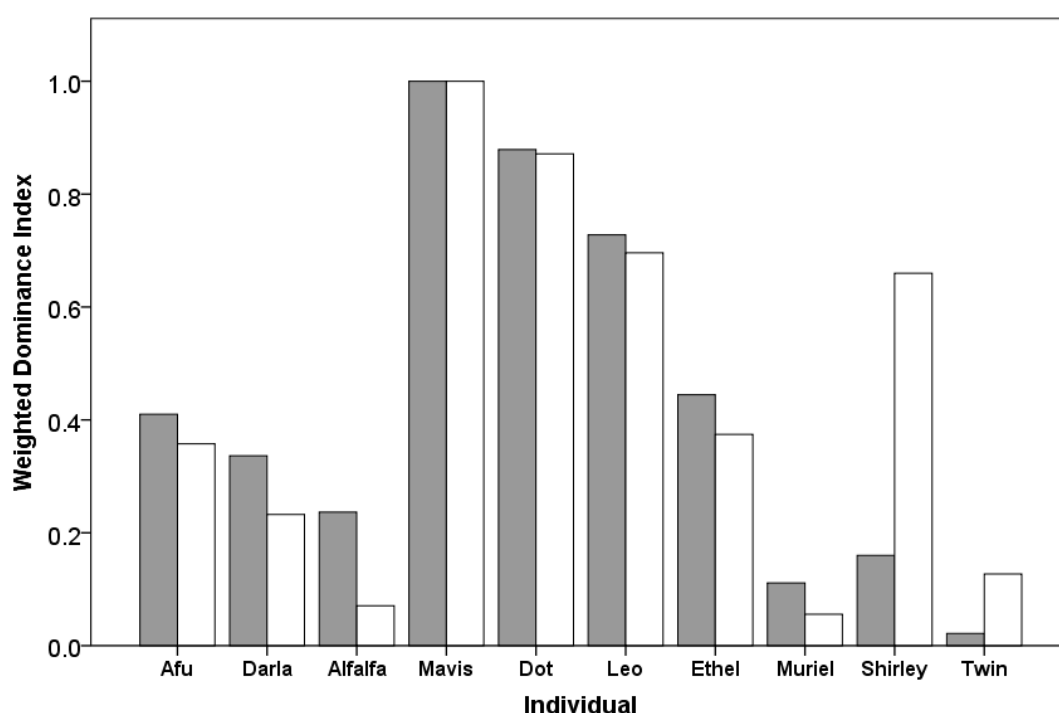


Figure 2: Weighted dominance index calculated from the number of wins and losses of agonistic interactions an individual is involved in, the higher the dominance index, the more dominant the individual. Columns are clustered depending on whether food was present: no food present (grey); food present (white).

Mavis (DI = 1) was most the dominant individual with the highest possible DI for both feeding scenarios as she never lost an agonistic interaction, closely followed by Dot then Leo. All three showed little change in dominance with and without food. Afu had the highest male DI during feeding (DI = 0.41) and non-feeding sessions (DI = 0.36), dropping the least when food was added. Muriel had the lowest female DI for feeding (DI = 0.06) and non-feeding (DI = 0.11), whereas Alfalfa had the most prominent drop of DI decreasing a third from feeding (DI = 0.24) to non-feeding (DI = 0.07). Only Shirley and the twin's DI increased when food was present, with Shirley's increasing by four times and the twins increasing by almost six times compared to non-feeding sessions (Fig.2).

Table 3: Individuals within each rank based on their Weighted Dominance Index for both feeding and non-feeding sessions. Individuals within each rank are in descending order of dominance.

Rank	No Food Present	Food Present
High	Mavis	Mavis
	Dot	Dot
	Leo	Leo
Medium	Ethel	Shirley
	Afu	Ethel
	Darla	Afu
Low	Alfalfa	Darla
	Shirley	Twin
	Muriel	Alfalfa
	Twin	Muriel

Social Network Analysis

All sociograms are highly connected as most nodes interact with all other nodes in both directions. For agonistic and allogrooming sociograms, individuals were clustered into three communities whereas they were only clustered into two for association however, the modularity was very weak with no actual communities found in this social group.

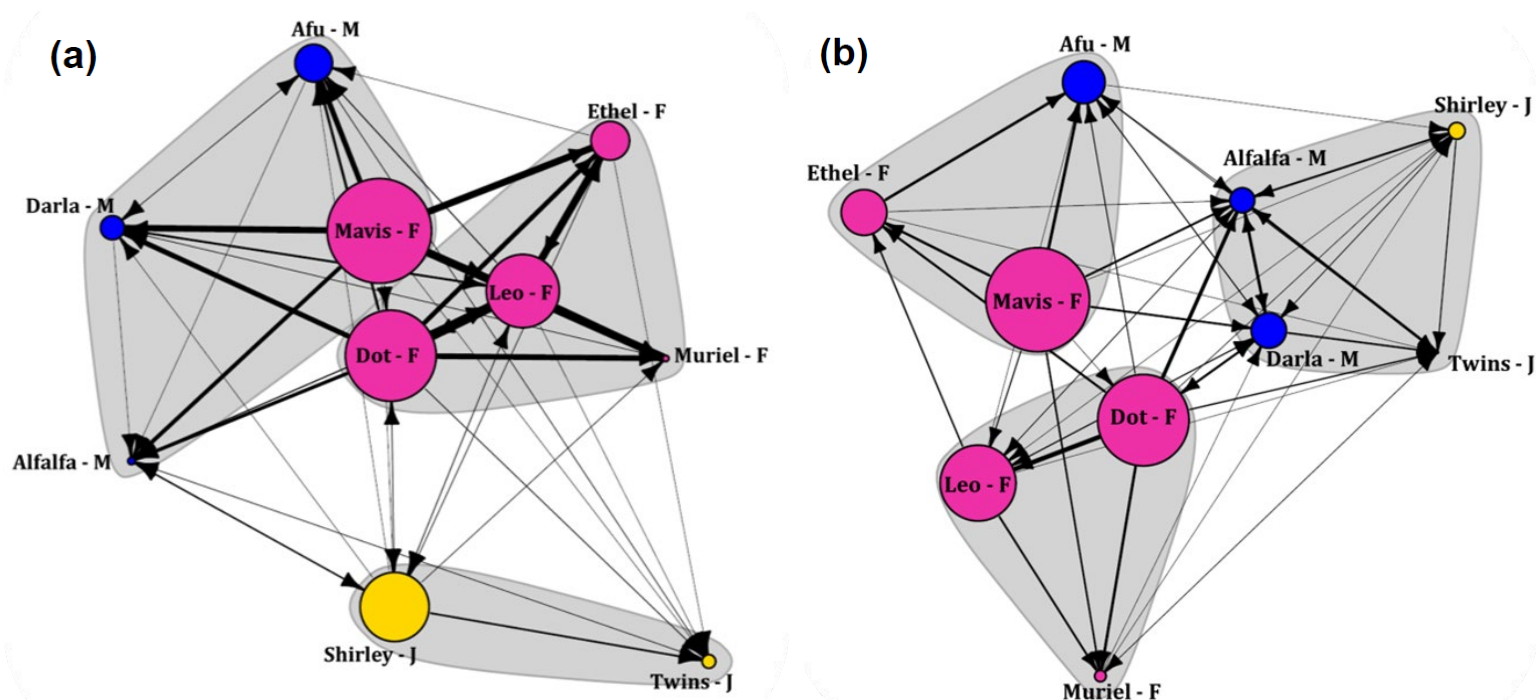


Figure 3: The social structure for: (a) directed aggression during feeding sessions; (b) directed aggression during non-feeding sessions. Each node is coloured depending on sex or age: females (pink/F); males (blue/M); juveniles (yellow/J). Nodes are weighted by the individuals weighted Dominance Index, the larger the node, the more dominant the individual. Edges are weighted on the number of counts that occurred between that pair, the thicker the edge, the higher the number of counts. Arrows indicate the direction in which the connection occurs. Shaded circles around nodes represent clusters with colour assigned randomly. Each network is force-directed using the Fruchterman-Reingold algorithm.

During feeding modularity was 0.015 (Fig. 3a), the first community consisted of only juveniles indicating that these directed and received the most aggression towards each other. The second community contained all females apart from Mavis. This community had very high eigenvector centrality coefficients (ECC) for aggression (Fig. 5) and a much higher number of aggressive interactions between all individuals compared to other communities. Muriel received the most and initiated the least aggression of all individuals. The third community consisted of all males and Mavis, Mavis directed large amounts of aggression towards the second cluster in addition to directing aggression towards the males, more so than other females.

When not feeding, there was a modularity of 0.036 for aggression networks (Fig. 3b), each of the three communities contained individuals with both high and low ECCs (Fig. 5). The first community contained Darla, Alfalfa and both juveniles which had the lower ECC of the community. The second community consisted of the second most dominant females, Leo and Dot and the least dominant, Muriel, who also had the lowest ECC for aggression. The final community consisted of the most dominant male and female, Mavis and Afu as well as Ethel.

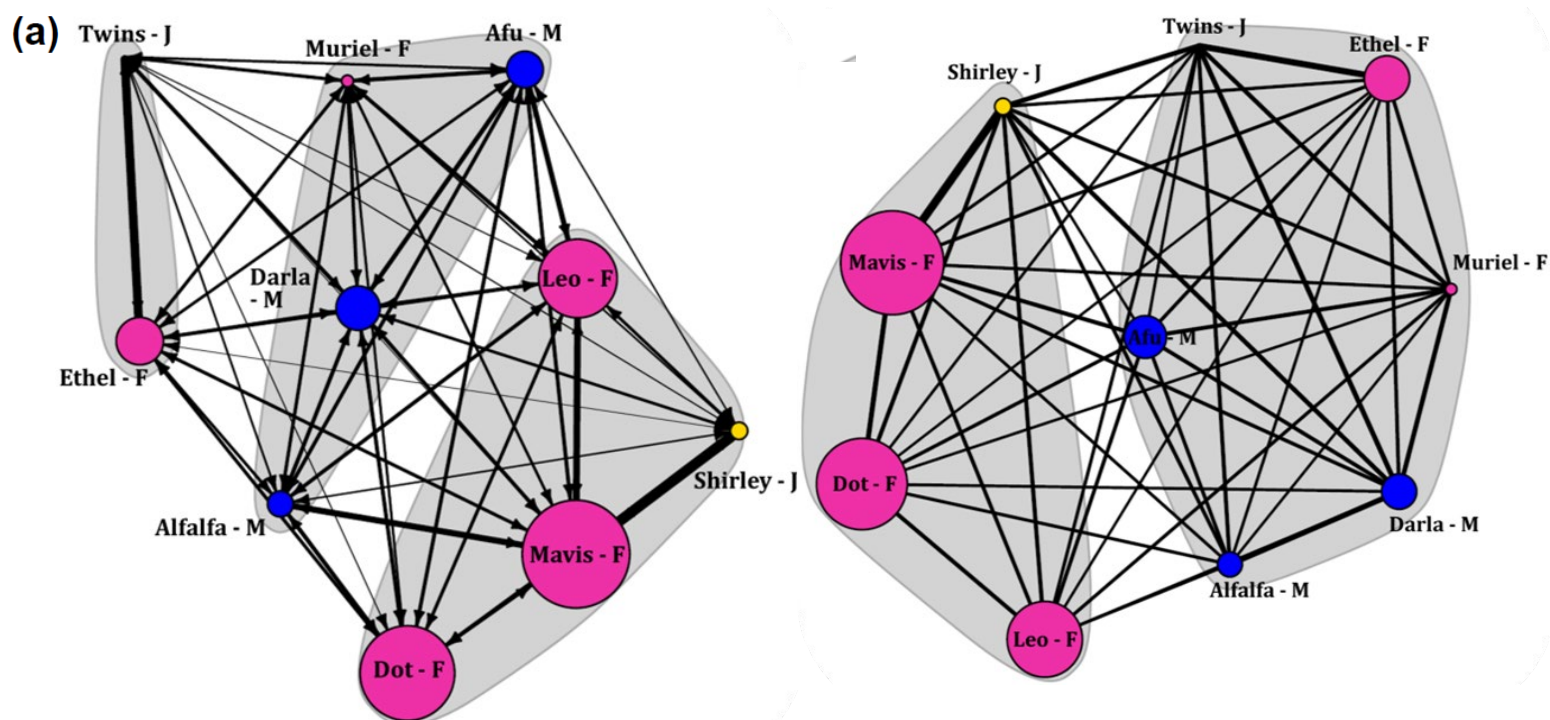


Figure 4: The social structure for: (a) directed grooming of conspecifics; (b) undirected association with other individuals. Each node is coloured depending on sex or age: females (pink/F); males (blue/M); juveniles (yellow/J). Nodes are weighted by the individuals weighted Dominance Index, the larger the node, the more dominant the individual. Edges are weighted on the number of counts that occurred between that pair, the thicker the edge, the higher the higher the number of counts. Arrows indicate the direction in which the connection occurs. Shaded circles around nodes represent clusters with colour assigned randomly. Each network is force-directed using the Fruchtermane-Reingold algorithm.

The allogrooming network had a modularity of 0.011, indicating that individuals in each community initiated and/or received grooming with those within their community more than those outside their community. One community consisted of Shirley and the most dominant individuals, Dot, Leo and Mavis. Within this cluster, a higher amount of grooming occurred between Mavis and Shirley, a similar level also occurred between Ethel and the twins who made up the second community, this pattern of increased counts was also true for association. The final community consisted of all three males and Muriel, the most subordinate female (Fig, 4a).

The association network had a modularity of 0.022, where communities indicated that individuals within each cluster associated more with each other. The same as allogrooming, the first cluster consisted of Shirley and the most dominant females whereas the second cluster consisted of the remaining subordinate males and females (Fig. 4b).

Eigenvector Centrality

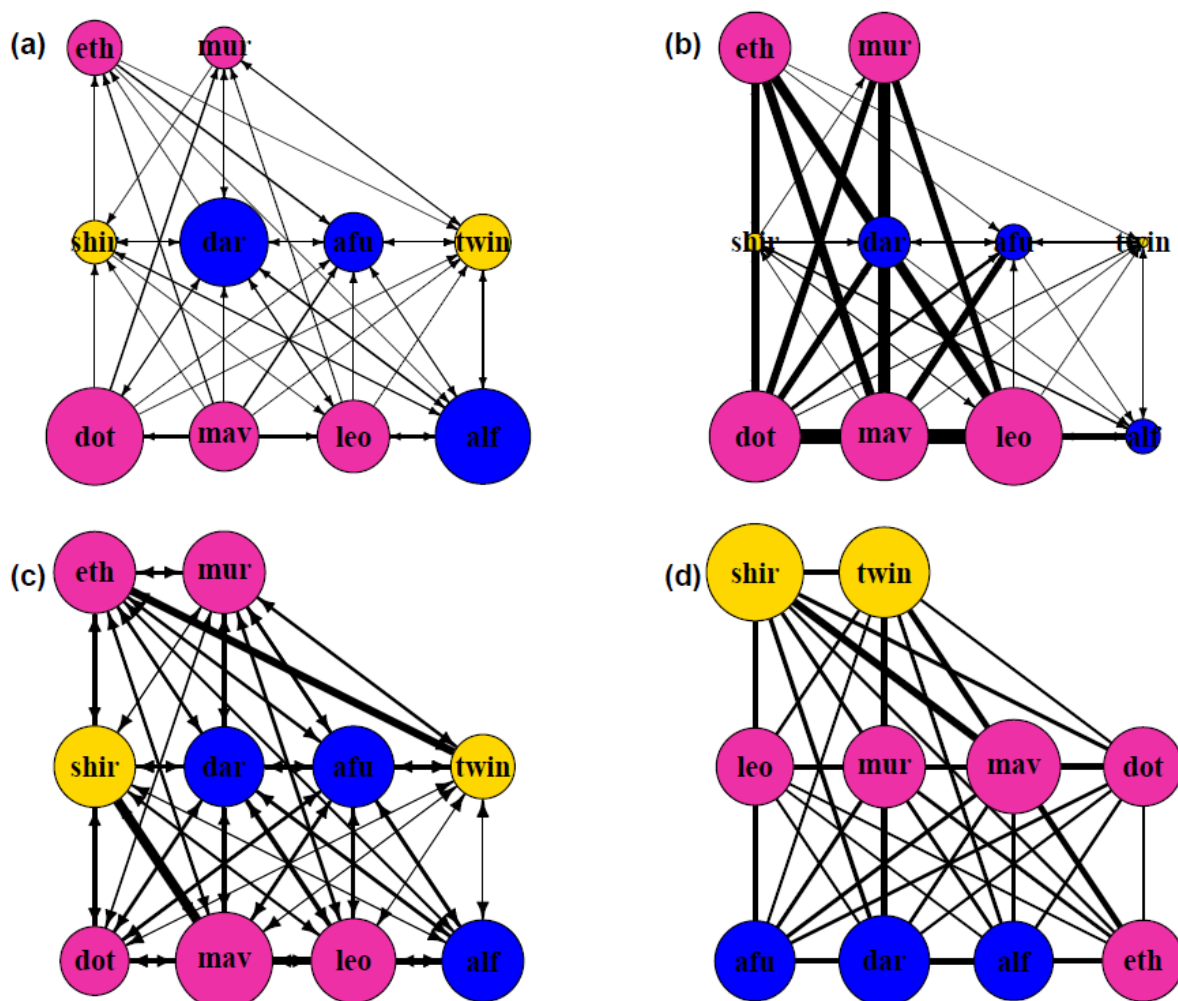


Figure 5: Eigenvector-centrality coefficient for individuals depending on different social behaviours: (a) directed aggression during non-feeding sessions; (b) directed aggression during feeding sessions; (c) directed grooming of conspecifics; (d) undirected association with other individuals. Nodes are coloured depending on sex or age: females (pink); males (blue); juveniles (yellow). Nodes are weighted by the individuals eigen-vector centrality coefficient, the larger the node, the higher the coefficient and therefore the bigger the influence that individual has on the group for that behaviour. The thicker the edge, the more connected two individuals are. Arrows indicate the direction in which the connection occurs. Each network is force-directed using the Grid algorithm. Individuals are abbreviated to the first three letters of their name fully listed in Table 1.

During non-feeding sessions, Dot (ECC = 1) had the biggest influence on the aggressive network, closely followed by Darla (ECC = 0.91) and Alfalfa (ECC = 0.98). All other individuals had a lower ECC ranging from 0.7-0.4 (Fig. 5a). For aggressive interactions during feeding, Dot, Mavis and Leo had very a high ECC ranging from 0.9-1, followed Ethel and Muriel (ECC = 0.7). Alfalfa, Shirley and the twins had a very low ECC (Fig. 5b).

All individuals had relatively high ECC for grooming, the highest of which being Mavis (ECC = 1) and the lowest being the twins (ECC = 0.6) (Fig. 5c). Similarly, there was even less variation in ECC for association with Shirley having the highest centrality (ECC = 1) and Leo having the lowest (ECC = 0.7) (Fig. 5d). All had a good influence on the social community for both affiliative networks.

Aggressive and Submissive Behaviours

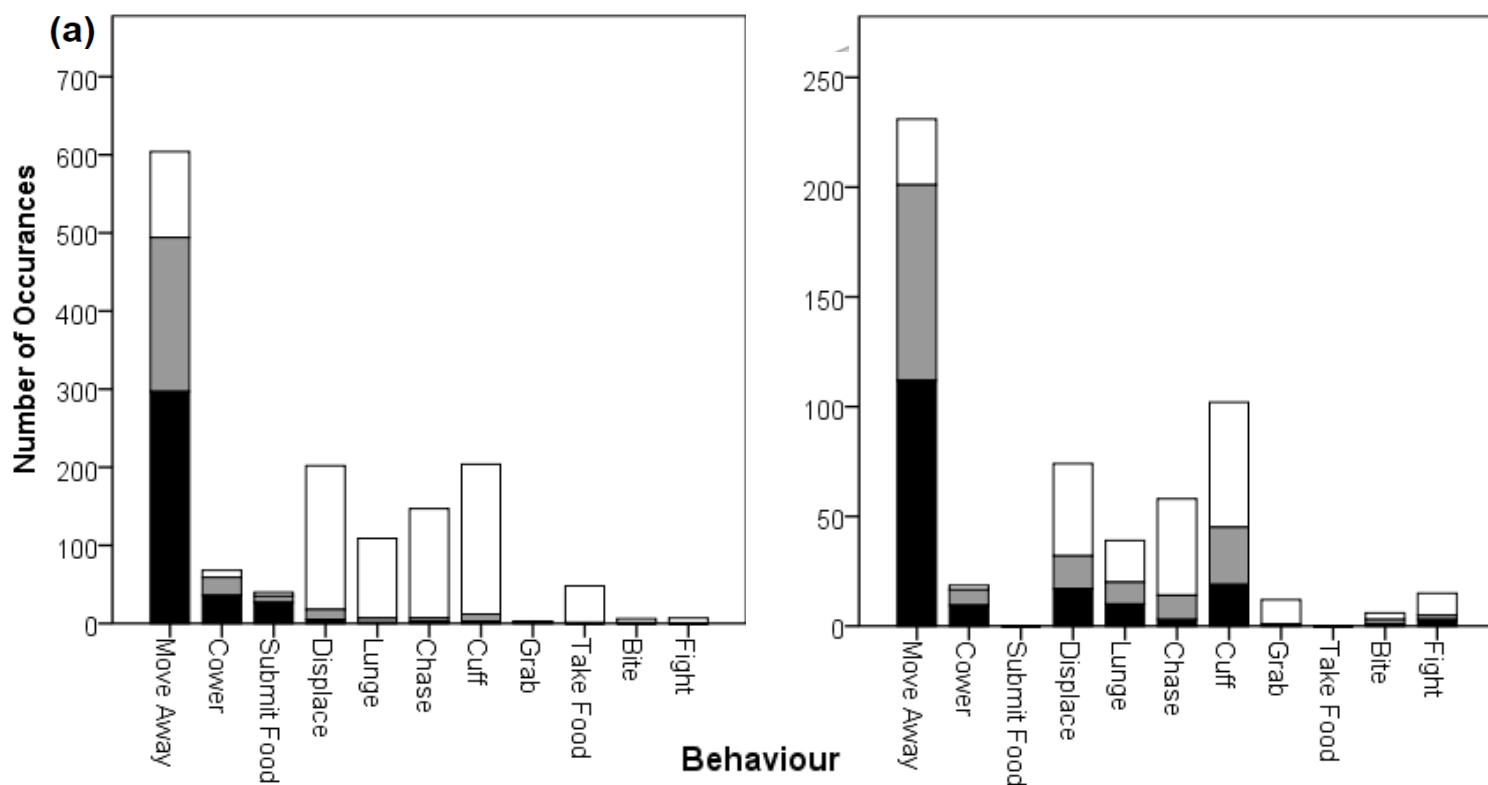


Figure 8: Distribution of aggressive and submissive behaviours produced when there was: (a) food present; (b) no food present. Bars are ordered from least to most aggressive behaviours from left to right, with the three leftmost bars representing submissive behaviours. Bars are stacked and shaded to illustrate the number of occurrences produced by each dominance rank for each behaviour: high (white); medium (grey); low (black).

There was a significant difference in the aggressive and submissive behaviours performed depending on rank during feeding (Chi-square test: $\chi^2_{18} = 862.05$, $P < 0.001$; Fig. 8a) and non-feeding sessions (Chi-square test: $\chi^2_{16} = 166.87$, $P < 0.001$; Fig. 8b). Using the adjusted significance level, the critical chi-squared value was calculated to be 10.83. There was a higher number of significant differences between observed and expected counts of aggressive and submissive behaviours during feeding compared to non-feeding sessions. For details see of which combinations of aggression and rank were significant, see Appendix Table A1 and Table A2.

Generally, during feeding, high ranking individuals showed significantly more aggressive behaviours and significantly fewer submissive behaviours than expected, with the opposite pattern found for medium and low ranks. The medium rank did not

show as extreme a significance in behaviours compared to the low rank, with no significant difference in taking or submitting food. Fighting and biting occurred much less frequently across all ranks and were not significantly different from the expected values. Cuffing was the most common aggressive behaviour at 192 for the high rank, closely followed by displacement at 184, then chasing at 140. Taking food was the lowest significant behaviour at 47 counts for the high rank, with no grabbing seen during feeding. Aggressive behaviours for medium and low ranks each occurred less than 15 times each, significantly less than expected.

During non-feeding sessions, no taking of food or allowing food to be taken (submitting food) occurred, with covering occurring significantly more than expected in low ranks. Only chasing occurred significantly more than expected closely followed by cuffing and displacing, only being performed by the highest rank. Chasing was significantly lower than expected in the low rank. The most common submissive behaviour that was most significant for all ranks was moving away, this was significantly higher in medium and low ranks and significantly lower in the high rank in both feeding scenarios.

Allogrooming

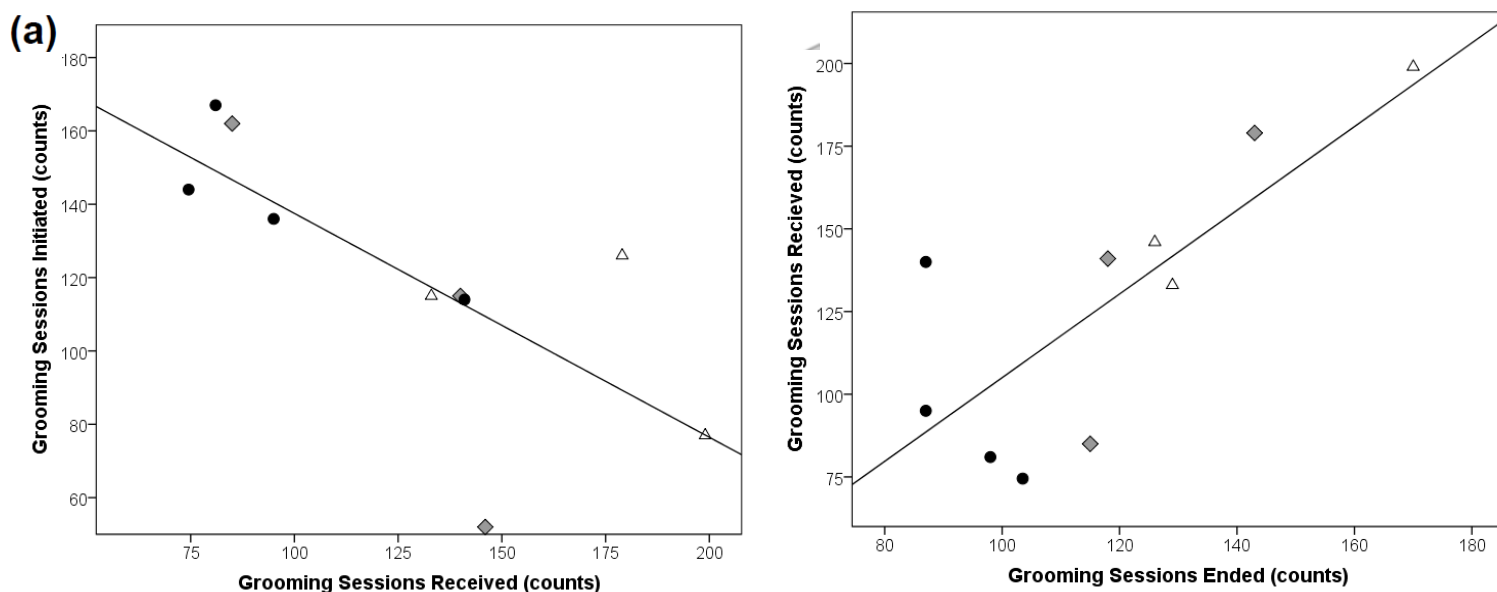


Figure 6: Relationship between the: (a) total number of times an individual received grooming compared to the number of times the same individual initiated grooming with a conspecific ($N = 11$); (b) total number of times an individual ended grooming compared to the number of times the same individual received grooming from a conspecific ($N = 11$). Points are coded depending on dominance rank: high (white/triangle); medium (grey/diamond); low (black/circle).

Table 4: Total counts of grooming initiated and received within each dominance rank.

Rank	Total Sessions Initiated	Total grooming Sessions Received
High	488	956
Medium	804	810
Low	1124	781

There was a strong significant negative relationship between the total grooming initiated and received depending on the individual (Spearman rank correlation: $r_s = -0.82$, $N = 10$, $P = 0.004$; Fig. 6a). As the number of times an individual initiated grooming increased, the number of times they received grooming decreased. This pattern was generally true for dominance where the more dominant the individual, the less they initiated grooming with the opposite pattern found for receiving grooming (Fig. 4a). Total grooming counts initiated decreased by around 300 and grooming counts received increased by around 100 with increasing rank (Table 4). There was also a significant positive relationship between receiving grooming and ending the grooming session (Spearman rank correlation: $r_s = 0.69$, $N = 10$, $P = 0.028$; Fig. 6b), the more an individual received grooming the more likely they were to end the grooming session, this pattern generally became more exaggerated with increasing dominance.

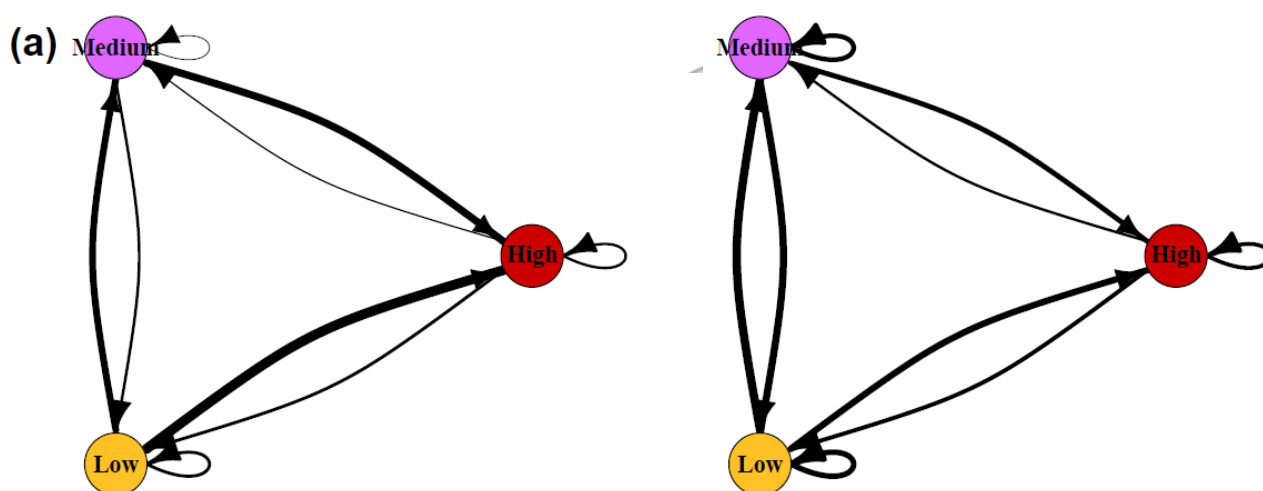


Figure 7: Frequency of grooming directed to certain areas of the body depending on dominance rank (a) lower half of the body; (b) upper half of the body. Each node is coloured depending on dominance rank: High dominance rank (red); Medium dominance rank (purple); Low dominance rank (yellow). Arrows indicate who the grooming was directed towards weighted by the number of occurrences, therefore the thicker the line, the higher the counts of grooming. Looped arrows indicate the number of time upper or lower grooming occurred between individuals within a rank. Each network is forced-directed using the Circle algorithm.

A negative relationship was found between the number of times individuals received grooming on the lower half of their body and the number of times an individual initiated grooming on a conspecific's lower half (Spearman rank correlation: $r_s = -0.96$, $N = 10$, $P = <0.001$; Fig. 7a). As an individual initiated grooming on the lower half of another more frequently, the amount they received in that area decreased. Individuals of a higher rank received grooming on their lower half more frequently than they initiated grooming in this area, with the opposite pattern found for lower ranking individuals. However, there was no significant relationship when comparing the amount of grooming an individual received or initiated on the upper half of their own, or another's body (Spearman rank correlation: $r_s = -0.35$, $N = 10$, $P = 0.327$; Fig. 7b).

Male Scent Marking

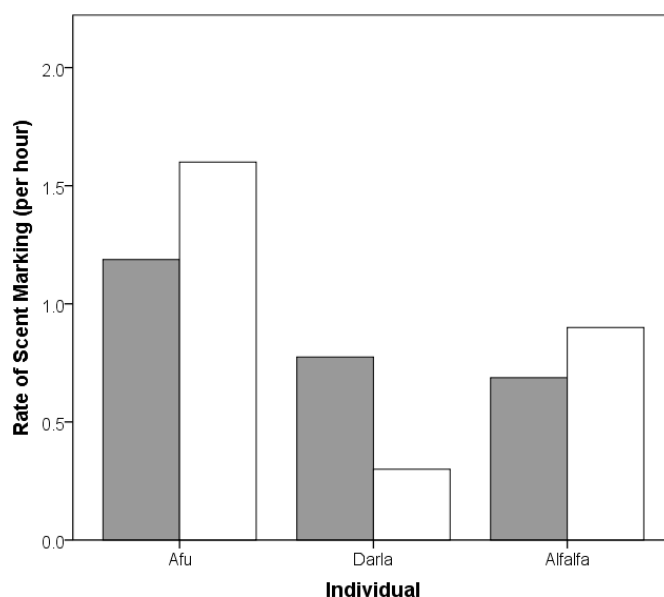


Figure 9: The rate of scent marking carried out by each male per hour in and out of feeding, bars are clustered on the presence of food, no food present (grey); food present (white).

Scent marking frequency was significantly different depending on the male (Chi-square test: $\chi^2_2 = 18.03$, $P < 0.001$; Fig. 9). Afu scent marked the most ($N = 111$), almost double that of Darla ($N = 65$) and Alfalfa ($N = 64$). However, there was no significant difference between the number of scent marks when comparing the interaction of food presence and the individual male (Chi-square test: $\chi^2_2 = 4.31$, $P = 0.116$). Nor did the total number of scent marks differ during feeding ($N = 28$) or non-feeding ($N = 215$) sessions (Binomial Test: $N = 240$, $P = 0.846$), with the hypothesis probability adjusted to 0.111 for non-feeding sessions.

Discussion

The results presented in this study confirm network structures vary depending on behaviour and individual characteristics. Most results did not greatly differ from wild lemur behaviour, matching the expected social hierarchy for this species, with females being the dominant sex and linear hierarchies within each sex (Wilson & Hanlon, 2010). All networks were highly connected, aggressive networks had a high variation in clustering and centrality, with more dominant individuals being more central, unlike affiliative networks which were more evenly distributed as these behaviours are beneficial to all (Tiddi et al., 2012). As predicted, more aggression occurred during feeding as this is a defendable resource all individuals wish to monopolise (Lu et al., 2008). More dominant individuals initiated more aggressive interactions but exhibited less extreme aggressive behaviours, whereas less dominant individuals showed more submissive behaviours to quickly end conflict and prevent injury (Pereira & Kappeler, 1997). As predicted, subordinates generally initiated more grooming to gain group acceptance (Tiddi et al., 2012). However, unexpectedly, subordinates commonly groomed accessible areas on higher-ranking individuals, possibly to reduce the risk of receiving aggression (Franz, 1999). Food did not influence male scent marking, instead the frequency increased with dominance to provide honest indicators of quality for female mate choice (Oda, 1999).

Dominance

There are many factors which affect wild ring-tailed lemur dominance (Bauer, 2004), one being sex which influenced dominance as expected as both sexes had linear hierarchies and females were the dominant sex, forming the highest rank for both feeding scenarios. This is because females need priority access to resources to increase their reproductive success (Petty & Drea, 2015). Relatedness affected dominance, as Mavis's matriline was more dominant than Ethel's, concurrent with previous research (Jolly, 1966; Wilson & Hanlon, 2010). In addition, mothers were always dominant to their offspring, this reduces direct competition between closely related individuals which share many of the same genes, thus benefiting their inclusive fitness (Hamilton, 1964; Bauer, 2004).

Furthermore, dominance generally increased with age caused by the increased knowledge of resources and fighting gained through life (Gould et al., 2003). This is known to increase centrality, as seen in Mavis, because it allows for knowledge to spread quickly through the group increasing overall group survivorship, beneficial for closely related groups like this one (Kulahci et al., 2018). Dominance dropped for Muriel as expected because of her age causing declining cognitive ability (Picq, 2007) and physical condition (Roth et al., 2004). However, age cannot be the only determinant of dominance as Leo is older but subordinate to Dot. Sub-adult ring-tailed lemurs initiate challenges towards dominant adults illustrating their physical ability in order to increase dominance later in life (Nakamichi & Koyoma, 1997; Bauer, 2004). This may be why now Dot is dominant over Leo as she was more aggressive when younger.

The order of dominance did not change greatly by the presence of food. Male and lower-ranking female dominance decreased the most during feeding, as expected, because they rarely won contests therefore lacked power to monopolise food (Nakamichi & Koyoma, 1997). The biggest change occurred in the juveniles, with their dominance increasing during feeding possibly to monopolise more food to reduce their risk of nutritional stress, as they require more energy per kilogram of body mass than adults (Chapman et al., 2012). Shirley's dominance was higher as she is from the dominant matriline (O'Mara & Hickey, 2014), in addition she is Mavis's only juvenile meaning she developed faster than the twins. This larger weight and strength can be used to her advantage in conflict (Sauther, 1992). As juveniles have little dominance over adults (Pereira, 1993) it explains why Shirley directed most aggression towards the twins.

Agonistic Social Networks

For both agonistic networks, the more subordinate an individual was the more aggression they received because aggression is used to ensure individuals recognise their social position, and for dominant individuals to reinforce their status as seen in the wild (Holekamp & Strauss, 2016). As a result, dominant individuals such as Mavis and Dot rarely received aggression because subordinates recognise they cannot win so do not waste energy by challenging them (Franz et al., 2015). Aggression was much higher during feeding because high levels of agonism commonly occur over contests for defensible resources, especially food suggested to be the most important resource influencing primate social systems (Saj et al., 2007).

During feeding, juveniles had low centralities and minimal group influence as they rarely initiated or received aggressive interactions with adults. It is uncommon for adults to risk injuring juveniles by directing aggression towards them in closely related groups like this one, because it can be detrimental to the aggressor's inclusive fitness (Whiten & De-Waal, 2018). Also, adults that are aggressive towards juveniles decrease their group acceptance because aggression does not demonstrate attractive characteristics to the group (Kaburu & Newton-Fisher, 2015). Unlike the juveniles, females had higher centralities than males, especially dominant females, because they directed aggression to both males, to prevent them stealing food, and other well-connected females to outcompete them (Bauer, 2004). Subordinate females directed aggression to males more than females, because it is easier to win against males when compared to more dominant females as males already have secondary access to food (Pereria & Kappeler, 1997; Curren et al., 2015). As a result, there is little benefit in males initiating competitions against females for access to food, explaining why males directed increased aggression towards each other.

Aggression occurred most frequently between the subdominant females, Dot and Leo, despite being closely related. Similar ranking individuals often direct more aggression towards one another because it is difficult for them to assess their chances of success (Smith & Price, 1973). This increased aggression aids the winner-loser effect, where those who win more disputes are more likely to win in future, thus becoming more dominant than the similar ranking individual (Hsu & Wolf, 2001). The aggression directed towards subordinates from these females may increase this effect further, as subordinates are even more likely to lose (Norscia & Palagi, 2015). Mavis did not direct as much aggression to these females despite being the same rank, however, there is little benefit in spending energy competing to increase her dominance when she is already the most dominant. Instead, she directed increased aggression to all, possibly to police overall group conflict important for group cohesion, highlighting that she is an important individual in maintaining this groups structure (Flack et al., 2006).

Outside of feeding there was a shift in the network as food was no longer the main source of competition. Darla, Alfalfa and Dot had the highest centralities but for opposite reasons, the low-ranking males received lots of aggression whereas Dot was dominant so initiated large amounts of aggression, both increasing their contact with highly connected individuals (Gould, 1996b). Ethel and Mavis were clustered with the breeding male, Afu, due to the increased aggressive interactions as a result of females rejecting his mating advances (Drea, 2007). This could explain why the juveniles were clustered with the subordinate males, as their frustration of not having access to breeding females caused them to assert aggressive sexual dominance over subordinate juveniles (Furuichi et al., 2013). The third cluster consisted of Dot, Leo and Muriel. Dot and Leo were more likely to be aggressive outside of feeding due to their similar rank as previously mentioned (Smith & Price, 1973). Muriel was the least dominant female with and without food as she rarely initiated aggression yet received and lost many from Leo, Dot and Mavis. Although primates direct increased aggression to ensure subordinates recognise their social position (Norscia & Palagi, 2015), this increases stress which could have caused Muriel to over-groom which was commonly seen throughout the study, highlighting that future management should target this issue.

Aggressive and Submissive Behaviours

As expected, both aggressive and submissive behaviours were higher during feeding with more aggressive behaviours exhibited by the highest rank (Kulik et al., 2015). Therefore, it makes sense that medium and low ranks showed more submissive behaviours to acknowledge they are the loser to reduce the severity of physical contests (Pereira & Kappeler, 1997). Unusually, primate studies rarely differentiate between behaviours making the severity of a groups aggression appear more extreme (Sussman et al., 2005), by acknowledging the different behaviours it can highlight greater details within social systems.

During feeding, less extreme aggressive behaviours were used more commonly, such as displacement, whereas extreme aggressive behaviours, such as fighting, were rarely seen. This suggests that disputes were easily settled and individuals recognise their social position in this group, because there is little benefit to escalating aggression and risking injury if an individual knows they will not win (Smith & Price, 1973). Furthermore, subtle aggressive behaviours can indicate more threat, so are commonly used by high-ranking individuals (King et al., 2008) because they have already achieved their dominance, therefore there is little additional benefit in spending energy on extreme aggressive behaviours (Sbeglia et al., 2010). Taking another's food occurred infrequently as food was spread throughout the enclosure, and subordinates generally picked up food and moved away, possibly a pre-emptive action to avoid aggression (Pereira & Kappeler, 1997).

During non-feeding sessions all behaviours dropped becoming more evenly distributed across ranks, as individuals had different desired resources which females did not have priority access to, for example mating (Cavigelli & Pereira, 2000). Chasing is energy expensive and was the only significant aggressive behaviour (Jolly et al., 2002). As desired resources during non-feeding were less abundant this increases their benefit, explaining why extreme aggression was higher as individuals were willing to incur the energetic cost (Georgiev et al., 2013). Cuffing and displacing were also common as they are less energy expensive ways of maintaining dominance (Shire, 2012). No conflict occurred over food despite being present possibly due to satiety signals removing the need to compete for food (Burnett et al., 2016). Moving away was the most common submissive behaviour with and without food as this behaviour obviously indicates submission, unlike cowering which could still result in injury (Franz et al., 2015).

Affiliative Social Networks

Both allogrooming and association have similar social functions across species, aiding group cohesion by improving communication and social bonds (Lehmann et al., 2007), however, evidence for this in lemurs is somewhat equivocal (Grueter et al., 2012). Instead, affiliative interactions can be directed towards specific individuals to gain personal social benefits such as higher dominance, tolerance over resources, or mate access (Schino & Aureli, 2008; Gabriel et al., 2014).

Both affiliative networks had similar clustering patterns. The dominant matriline formed one cluster in both networks, this increased affiliation can be explained by individuals trying to increase their indirect fitness by helping closely related kin

(Hamilton, 1964). Allogrooming increases groomee fitness by reducing parasite load (Akinyi et al., 2013) and association aids energy efficient thermoregulation by reducing the surface-to-volume ratio, which decreases heat loss (Terrien et al., 2011). However, caution should be taken as primate affiliation sometimes shows no difference in frequency between kin and non-kin (Bergman et al., 2003). Primates also use affiliation for reconciliation after agonistic interactions (Fairbanks, 1976; Perry et al., 2008). It has been debated whether ring-tailed lemurs adopt reconciliation (Kappeler, 1993) however, more recent research on their wild counterparts discovered it can occur during the breeding season when higher agonistic interactions occur (Palagi et al., 2005). This supports this study which took place during this time in addition to more affiliative interactions occurring between groups who were more aggressive.

The main difference in the affiliative networks was that Ethel and her offspring were clustered separately from lower ranking individuals in the allogrooming network. Although they also associated more frequently, it was not different enough to create a separate cluster. This separation in allogrooming resulted in Muriel and the males being clustered together. If Ethel did not have offspring to care for, it is expected for her to be clustered the same as the association network as she still frequently interacted with these individuals.

The increased allogrooming between Ethel and the twins suggests it plays a bigger role in rearing offspring than association. Previous research found that allogrooming juveniles increases their rate of development and social skills, helping to increase their acceptance within the group from a younger age (Lonsdorf, 2017). This acceptance is more important to the twins than Shirley as they are part of the subordinate matriline so have an increased likelihood of receiving aggression. This explains why Mavis and Shirley remained within a larger cluster despite frequently grooming each other, because Shirley is part of the dominant matriline so does not require the extra grooming to aid group acceptance. It is common for mothers and their offspring to have heightened affiliative interactions to increase offspring survival, this is caused by the mother-infant bond, formed via opioid stimulation to receptors in the ventral striatum which create a reward-fulfilling activation (Broad et al., 2006). However, little to no affiliation occurred from mothers to juveniles that were not their own. Although grooming another's young can provide social benefits (Henazi & Barrett, 1999), there is little for Mavis as she is most dominant, and also to Ethel who has twins which require double the energy to rear (Norscia & Palagi, 2015).

Increased affiliative interactions did occur across clusters. For allogrooming this occurred between Alfalfa, Mavis, Dot and Leo. Alfalfa is Mavis's son and Dot and Leo's brother so may be for kin-related benefits however, allogrooming was mainly initiated by Alfalfa so is likely to be attempts to increase social acceptance (Port et al., 2009). For association, the juveniles may have had a slightly higher connectedness as this bonding can aid their social development (Whiten & De-Waal, 2018). Increased connectedness across clusters commonly occurred for association, contradicting the hypothesis that dominant individuals would associate more. However, this lacking bias between pair-wise interactions suggests association plays less of a social role than allogrooming, so is not heavily relied upon by subordinates to gain social benefits from dominant individuals (Fedurek & Dunbar, 2009).

Unusually, juveniles were highly central in association networks due to having increased connectedness with seemingly random individuals. This could be because juveniles have high surface-to-volume ratios, so need to huddle more to conserve energy in English Autumn temperatures (Wright, 1999). It may also be others increasing their rank-related benefits. Although it was previously thought that only mothers cared for offspring (Jolly, 1966), alloparental care benefits all by increasing mating opportunities for males, maternal experience for females with both sexes gaining an increase in group social acceptance and dominance (Gould, 1992; Norscia et al., 2009). This explains why Afu directed allogrooming to the twins and Darla associated more with Shirley. Darla's association with Shirley may have been more beneficial than attempting to increase dominance by associating with Mavis, as he risked receiving aggression (Pereira & Kappeler, 1997). However, Alfalfa groomed Mavis more than Darla but remained less dominant, suggesting that alloparental care has a greater influence on dominance than allogrooming however, this requires further testing.

Allogrooming

This study showed that grooming patterns varied with dominance as previously hypothesised. Lower ranking individuals initiated allogrooming most and received the least with the opposite found for dominant individuals as seen in wild lemurs, this bias supports growing evidence that allogrooming plays as large a social role in lemurs as anthropoids (Dunbar, 1991). The hygienic benefits that allogrooming provides to the dominant individual increases their tolerance of subordinates in return, as those who initiate more affiliative behaviours receive less aggression (Gould 1996a; Norscia et al., 2009). This could contribute to why Ethel and Muriel received heightened aggression from dominant females during feeding, as they were rarely affiliative towards them. Dominant individuals rarely initiated grooming and frequently ended these interactions because there is less social benefit for them as they are already dominant, so do not need to spend as much energy on trying to increase dominance further (Hobson & DeDeo, 2015).

As allogrooming serves a hygienic function it should occur on areas that are inaccessible to the groomer (Grueter et al., 2012), identified in ring-tailed lemurs as the head, face and neck (Barton, 1985). However, in this study subordinates directed more allogrooming towards the lower-half of higher ranks. Research has shown ring-tailed lemurs also allogroom the base of another's tail due to the increased matting from urine marking (Hutchins & Barah, 1976). This may have been the chosen location for subordinates, to avoid the risk of grooming near the face area because this face to face contact can be mistaken for a challenge of dominance (Mazur, 2013). This increased risk of conflict may outweigh the benefits of a stronger social bond (Mielke et al., 2018). In addition, allogrooming the lower-half adds additional protection against injury by having the vulnerable ventral side facing away from the dominant individual (Borries, 1992). This could also be why allogrooming networks had a more biased distribution of interactions between group members compared to association networks, because there is a greater cost related to allogrooming compared to simply associating near a dominant individual. Unusually, there was no significant difference between initiating and receiving allogrooming on the upper-half of the body. However, in some primates, eye contact increases intimacy and bonding during social interactions (Franz, 1999), explaining why upper-half allogrooming

occurred commonly between middle and low ranks as they are less aggressive, suggesting the benefit of increased bonding outweighs the risk of injury.

Scent Marking

This study found no differences in scent marking depending on the presence of food, indicating its role is not for food competition. Previous research has shown that scent marking in lemurs is used for territory defence (Gaspari & Crockett, 1984), which changes to represent dominance when living in high densities (Clutton-brock & Harvey, 1978), common in captive settings with individuals limited by their enclosure. Scent marking is thought to be used instead of physical agonistic behaviours between males, as female primates preferentially select non-aggressive males over aggressive higher-ranking males (Kaburu & Newton-Fisher, 2015). This evidence supports this study as males were less aggressive than females and Afu, the dominant breeding male, scent marked significantly more than the other males, as hypothesised. However, there is contradicting evidence as to if scent marking increases with dominance (Kappeler, 1990; Gould & Overdorff, 2002). This study took place during the breeding season when signals in male ring-tailed lemur scent marks change, providing honest indicators for female mate choice via their level of heterozygosity, which accurately predict health and survivorship, the genetic distance between individuals (Oda, 1999) and information for male competitors, such as location (Gould & Overdorff, 2002). This chemical component is costly to produce (Johansson & Jones, 2007) which may be why Afu scent marked the most, as he was the oldest and largest male so could afford the cost of more frequently scent marking. Some studies may not have found this as they occurred over a longer period which may have cancelled out differences during the breeding season.

Conclusion

Overall, this study has provided an insight into SNA in captive ring-tailed lemurs which varies with agonistic and affiliative behaviours. More dominant individuals had a greater influence on agonistic networks however, this was not as important for affiliative networks. All social interactions could be explained by individuals acting to increase their benefits within the group, be this maintaining dominance, increasing mating opportunities or simply to avoid aggressive attacks. Behaviours did not differ greatly from their wild counterparts indicating a high standard of captive management is upheld at Bristol Zoo Gardens. SNA is a rapidly growing area of research influenced by a multitude of factors such as age, sex and experience, as illustrated here and is effective when used in combination with more classic data analysis. There was not enough data in this study to test all factors as the sample size was too small with data collected over a limited period through the breeding season. Future research would pay to investigate how specific aspects of affiliative and agonistic interactions differ in providing social benefits and which are more important for social structuring, whilst looking at larger groups over a longer period to see how patterns vary through time and between different captive groups. From this research, general rules of how each factor contributes to influencing centralities and social network structure could be used to predict social interactions, such as where aggression may occur, which individuals are most influential or, if any individuals are isolated from the group. Thus, providing a better understanding of lemur social behaviour to help aid future captive management.

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Appendices are available as ‘supplementary files’ (please see download area)