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Social dynamic analysis in a true matrilineal mandril (Mandrillus sphinx) colony

João Paulo Barros Pacheco
Dissertação de Mestrado apresentada à
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FC

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João Paulo Barros Pacheco

Mestrado em Ecologia e ambiente
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Orientador
Catarina Casanova
Professora Associada, Instituto Superior de Ciências Sociais e Políticas da
Universidade de Lisboa (ISCSP-ULisboa)

Coorientador
Nuno Monteiro
Investigador, Centro de Investigação em Biodiversidade e Recursos Genéticos
(CIBIO-InBIO)

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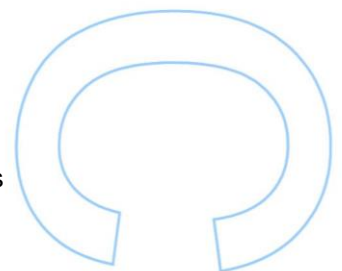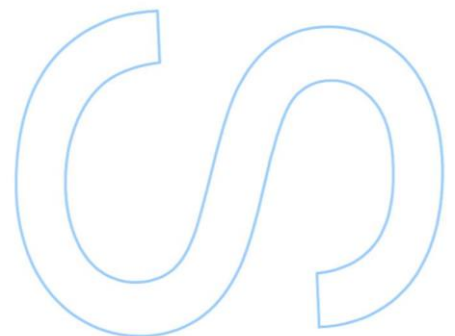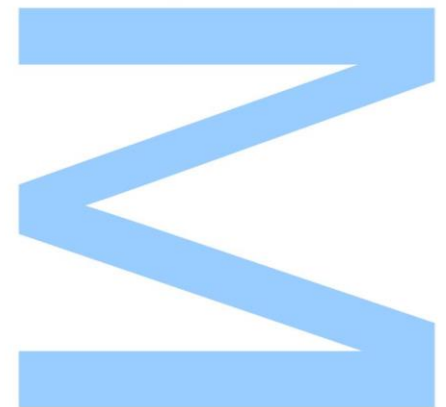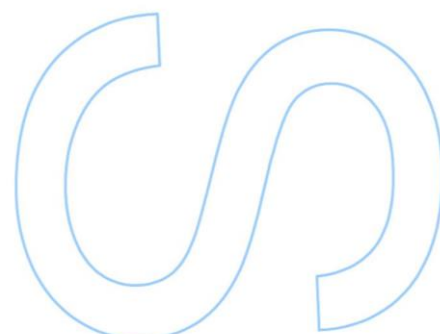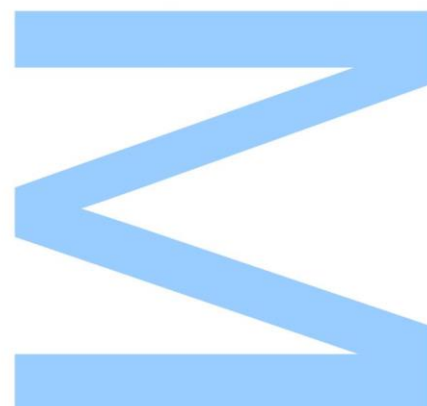
Todas as correções determinadas
pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, _____/_____/_____

"Closeness to animals creates the desire to understand them, and not just a little piece of them, but the whole animal. It makes us wonder what goes on in their heads even though we fully realize that the answer can only be approximated"

-   **Frans de Waal**

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Resumo

O sucesso reprodutivo dos primatas não-humanos é fortemente influenciado pelas interações sociais estabelecidas entre indivíduos, em particular, pela alocatagem que ocupa um papel central na vida dos indivíduos e das comunidades. Entre os cercopitecínios, a alocatagem, para além de promover a diminuição de "stresse", pode ser vista como uma "mercadoria" (de acordo com a Teoria dos mercados biológicos), podendo ser trocada por outras mercadorias/benefícios. Neste estudo foram estudadas as dinâmicas sociais de uma colónia de mandris. Os mandris são uma espécie cientificamente pouco conhecida e os dados do presente trabalho recolhidos em 2020 (N = 413 amostras focais, correspondentes a mais de 100 horas de observação) proporcionam uma boa oportunidade para estudar as dinâmicas socias de uma colónia matrilinear verdadeira de mandris, alojada no Badoca Safari Park (Sines, Portugal). Tendo em conta informação anterior a 2020, foi ainda possível realizar uma análise cronológica das dinâmicas sociais da colónia. Os resultados mostram que, entre os mandris observados, alocatagem foi de facto usada como um "recurso", sendo trocada por outras "mercadorias" (ex.: tolerância social ou acesso a alimento). Os resultados também demonstram que as relações sociais estabelecidas entre os indivíduos desta comunidade podem ser mantidas ao longo de extensos períodos (vários anos), confirmando a ideia da existência de mecanismos emocionais como o "emotional book-keeping mechanism" observados em outras espécies de cercopitecídeos. Ao melhorar o nosso conhecimento sobre as dinâmicas sociais desta espécie de primatas não humanos pouco conhecida, este estudo contribui para o conhecimento do comportamento social de uma espécie cuja população se encontra em risco de extinção devido à perda de habitat e caça ilegal.

Palavras-chave:

comportamento animal; mercado biológico; ranking; inclinação da hierarquia; modelo de Seyfarth; troca de recursos

Abstract

Social interactions have been shown to have a deep effect on the fitness of non-human primates, contributing to both their health and wellbeing. Amongst these animals, grooming behaviour is considered the cement of social relationships and has a central role in the life of individuals. For cercopithecoids, grooming may be seen as a tool that promotes stress relief and that can be traded for other commodities. This study is a contribution to better understand the social dynamics of grooming relationships in a true matrilineal colony of mandrills (*Mandrillus sphinx*) housed at Badoca Safari Park (Sines, Portugal). Data was collected via a focal sampling protocol, conducted during two consecutive months, in 2020 (N=413 focal samples, corresponding to more than 100 hours of observation). As the access to previous data from the same colony was available, a chronological view of the group's social dynamics was made possible by this study by conducting a follow up study. Results showed that grooming may be used as a commodity and therefore able to be exchanged for grooming or other currencies (social tolerance and access to food). This thesis also showed that partnerships can be maintained over long periods of time (several years), supporting the idea that mandrills use an emotional bookkeeping mechanism. By better understanding grooming social dynamics, I hope to improve the knowledge of the social behaviour of primates whose populations currently face the risk of extinction due to habitat loss and hunt for bushmeat.

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List of abbreviations

AR – Arms reach

ARE – Arms reach while eating

DI – Dominance index

CI – Concordance index

SEGC - Station d'Estudes des Gorilles et Chimpanzés

CIRMF - Centre International de Recherce Médicales, Franceville

H' - Shannon Weaver index

DS – David's score

normDS – Normalized David's score

RR - Relative ranking

ND – No data

1. Introduction

The long-term conservation of a species demands deep knowledge about its way of living. Besides knowing the features of the habitat where a specific group of primates live along with their diet, it is also important to learn how a particular species behaves. In primates (in this dissertation I will address all non-human primates as primates, and human primates as humans), the social behaviour is a pillar component of the community even affecting the fitness of individuals [baboons (Silk *et al.*, 2003; Silk *et al.*, 2010), chimpanzees (Wittig *et al.*, 2016), macaques (Schulke *et al.*, 2010)]. Primate's social interactions are important since the way of living and survivability depends on the exchange of affiliative behaviour (Brent *et al.*, 2013b; Silk *et al.*, 2003).

1.1 Social interactions

Social ties are present in every aspect of human's life. Such ties are critical components of human's fitness (Holt-Lunstad *et al.*, 2010; House *et al.*, 1988). Fitness is a concept used in many different biology fields. In the case of social behaviour, fitness can be used to describe the consequence of social relationships. Trivino and de la Rosa (2016) argue that fitness is not limited to a mathematical analysis regarding the number of offspring, but can actually, be defined as "*a causal disposition resulting from the non-linear combination of environmentally relative functional dispositions oriented towards an effect (surviving and reproducing) which is reached once the combination of these dispositions exceeds a certain threshold*" (Trivino and de la Rosa, 2016, p. 4).

Nevertheless, social ties are not exclusive traits of humans. These are important elements for the fitness, health and wellbeing of other species such as baboons (Silk *et al.*, 2003; Silk *et al.*, 2010), chimpanzees (Wittig *et al.*, 2016), macaques [*Macaca assamensis* (Schulke *et al.*, 2010)], horses (Cameron *et al.*, 2009), rock hyrax [*Procavia capensis* (Barocas *et al.*, 2011)] and even birds such as the greater ani [*Crotophaga major* (Riehl and Strong, 2018)]. A social bond can be seen as a relation between individuals where co-operative exchange occurs (Cheney, 2011). These co-operative exchanges are likely promoted by repeated interactions between partners which may evolve and eventually stabilize, into direct and indirect reciprocity (Boyd and Richerson, 1989; Nowak *et al.*, 2010; Trivers, 1971) leading to the establishment of differentiated relationships (Snyder-Mackler *et al.*, 2020). When analysed in humans, social relationships ranging from close or intimate partners to distant

associates form a continuum of complex social networks characterized by social ties of different preferences and degrees of reciprocal exchange (Apicella *et al.*, 2012; Dyble *et al.*, 2016). These intrinsic components of human networks are theorized to form dyadic co-operations, facilitating group integrated actions and even unique large-scale co-operations (Apicella *et al.*, 2012) through social interactions and differentiated social relationships. Social interactions and differentiated social relationships between individuals are also maintained by other group-living species (Snyder-Mackler *et al.*, 2020). Besides maintaining differentiated social relationships, some group-living species also engage in collective actions and group-level co-operative acts with in-group members (Arseneau-Robar *et al.*, 2017; Langergraber *et al.*, 2017; Majolo *et al.*, 2020; Mirville *et al.*, 2018; Samuni *et al.*, 2019a; Willems and van Schaik, 2015).

Recent studies have helped us to better understand the effect of differentiated social relationships in the lives of non-human animals (Crockford *et al.*, 2012; Fuong *et al.*, 2015; Kern and Radford, 2016; Schel *et al.*, 2013). Differentiated social relationships can result in a wide variety of benefits for both partners (Crockford *et al.*, 2012; Fuong *et al.*, 2015; Kern and Radford, 2016; Schel *et al.*, 2013). They may promote dyadic co-operative tasks associated with fitness such as improved defence against predators or other threats (Crockford *et al.*, 2012; Fuong *et al.*, 2015; Kern and Radford, 2016; Schel *et al.*, 2013) or even alloparental care (Gero *et al.*, 2009; Nam *et al.*, 2010; Samuni *et al.*, 2019b). Despite our increasing understanding of social relationships in non-human species, evidence on the effects of these relationships on group-level co-operation and collective actions remains scarce (Samuni *et al.*, 2021).

Co-operation between group members brings important benefits that can impact the survivability of individuals. One of such benefits is the transference of information between individuals: detection of threats by one or more individuals (detectors) and the transference of that information to non-detectors (the outcome of this transference of information between detectors and non-detectors is referred to as collective detection) is hypothesised as being an important benefit of group-living social vertebrates (Bednekoff and Lima, 1998; Lima, 1996). In primates, information transference is well developed. When in the presence of a predator, specific individuals warn the rest of the group through alarm calls capable of spreading the information to a large number of individuals (Caro, 2005; Frechette *et al.*, 2014) with one of the earliest studies of this behaviour coming from Struhsaker (1967) with vervet monkeys (*Chlorocebus pygerythus*). Such a well-developed capacity of information transference may facilitate bonding between group individuals (Cowlishaw, 1992, 1996; Geissmann and Orgeldinger, 2000; Mitani, 1988), and despite the subject of how information transference

affects bonding remains understudy, the effective transference of information between group members still requires some degree of sophistication involving cognitive abilities.

1.2 Cognitive abilities and social traits

The cognitive abilities of primates can tell us much about the way they interact with each other. To understand the information transfer in primates or other animals one must also understand how and why their cognitive abilities evolved. One widely accepted explanation for the evolution of advanced cognitive abilities in animals, and especially in primates, is the "social brain" hypothesis. This hypothesis states that the group-living environment was an important factor that led to the development of complex cognitive capabilities resulting in a complex brain, especially the neocortex region (Dunbar, 2003; Dunbar, 1992; Dunbar, 1998; Humphrey, 1976; Whiten and Byrne, 1988). The tendency of primates to seek the company of conspecifics is believed to be the result of evolution under predation pressure according to the predation defence hypothesis (Sterck *et al.*, 1997; Van Schaik, 1983; Van Schaik and Van Hooff, 1983). However, defending resources in a cooperative way (mainly by females) is another model that explains the option for group living amongst primates (Wrangham, 1980). Despite all advantages, group living promotes a range of specific cognitive challenges (Dunbar, 2003). These challenges include keeping track of the interactions between group members, changes in dominance relationships and formation of alliances and relationships between other individuals of the group (Bergman *et al.*, 2003; Cheney and Seyfarth, 1990; Dasser, 1988; Dunbar and Shultz, 2007; Range and Noë, 2005; Shultz and Dunbar, 2007; Shultz *et al.*, 2011).

1.3 Social bonds and fitness

By living in groups, and interacting with group members, social bonds are expected to rise between individuals. Such social bonds are not randomly created, and individuals focus their efforts on bonding the most profitable potential partner in order to increase their fitness (Hammerstein and Noe, 2016). It is widely accepted that, amongst humans, social integration (Holt-Lunstad *et al.*, 2010; House *et al.*, 1988) and socio-economic status (Stringhini *et al.*, 2017; Wilkinson and Marmot, 2003) are some of the most important predictors of mortality risk. In the last few decades, a similar correlation, this time between fitness and social environments, has been unravelled in primates (Archie *et al.*, 2014; Blomquist *et al.*, 2011; Brent *et al.*, 2017; Ellis *et al.*, 2019; Lehmann *et al.*, 2016; McFarland and Majolo, 2013; Silk

et al., 2010; Thompson and Cords, 2018; van Noordwijk and van Schaik, 1999). Indeed, studies have stressed the importance of social bonds in different primate species (Silk, 2012) including humans (Holt-Lunstad, 2017; Steptoe *et al.*, 2013). Yet, the relationship between social connections/networks and fitness remains to be fully comprehended amongst primates (Ellis *et al.*, 2019).

To recognise the individual benefits of social connections, one must first understand what is a social connection and how intimate or "well connected" individuals actually are (Ostner and Schülke, 2018). Being a "well connected" individual may be achieved via four different social connection types: (i) social integration; (ii) dyadic connectedness; (iii) structural connectedness; (iv) and direct connectedness [see Ellis *et al.* (2019) for a deeper analysis of each type of social connection]. Here, I will explain those who are in a certain way directly or indirectly discussed in this dissertation: social integration and dyadic connectedness.

It is important to analyse if an individual is socially integrated or socially excluded. A socially integrated individual is an individual that engages in a high frequency of interactions with others and/or interacts with a high number of partners. When measuring the social integration of an individual, the identity of the social partners is not an important element to take into account. Besides, when comparing two individuals with a similar rate of interactions, individuals that interact with a higher number of different partners and individuals that interact with fewer different partners are considered equivalent. A socially integrated individual may also possess a large number of weak (infrequent or transient) social partners (Granovetter, 1973). This type of social connection is considered beneficial to the individual because it helps individuals become socially tolerated by others giving individuals many different benefits such as access to contested recourses or spatial locations increasing their fitness by decreasing the likelihood of injuries or death (Barrett *et al.*, 1999; Henzi and Barrett, 2007; McFarland *et al.*, 2015).

In dyadic connectedness the identity of social partners is important. Relationships are built upon a series of interactions with specific individuals. Affiliative dyadic relations may be considered to be analogous to friendships [see Silk (2002); later used by Brent *et al.* (2014) and Hruschka (2010)]. When analysing dyadic interactions, the focus must be directed towards the most frequent or consistent partners. Consistent and frequent interactions between individuals are beneficial to both partners because they increase the efficacy of coordinated behaviours (Croft *et al.*, 2006; Dunbar and Shultz, 2010) and provide opportunities for mutualism or reciprocal exchange of interactions/services (Gilby, 2012; Schino and Aureli, 2017). Such relations provide a strong social environment and lead to the necessity and challenge of primates to form and maintain social bonds (Curley and Keverne, 2005; Dunbar and Shultz, 2010) via gregarious behaviours.

1.4 Social organization, hierarchy, and grooming exchange

1.4.1 Group Living: organization and hierarchy in primates

Although group living is not a rare occurrence in mammals, it is very common amongst primates (Alexander, 1974) as it brings obvious benefits to the survivability of group members. In female kin-bonded Cercopithecidae species, the investment and preservation of strong, stable and equitable social bonds (Silk *et al.*, 2010; Wrangham, 1980) has shown to increase the fitness of group members (Brent *et al.*, 2011; Crockford *et al.*, 2008; Silk *et al.*, 2010; Wrangham, 1980).

Despite the advantages of sociality, living in a group allows the emergence of conflicts and competition between group members. Over the years, evidence has been gathered that these advantages and disadvantages are not always equally distributed among group members (Hirsch, 2007; Quinn and Cresswell, 2006; Tkaczynski *et al.*, 2014; Viscido and Wethey, 2002). Higher ranking individuals will most likely spend most of their time in advantageous positions [such as centralized positions of the tridimensional space occupied by the group – based on the selfish herd theory by Hamilton (1971)] decreasing both the odds of being exposed to predators [predation risk (Krause, 1994; Stankowich, 2003; Van Schaik, 1983)] and the needs of spending time vigilant to external danger (Burger *et al.*, 2000; Janson, 1990; Petit and Bildstein, 1987). In group species characterized by a dominance hierarchy, high-ranking individuals will normally occupy places that provide advantageous spatial positions among the group (Hall and Fedigan, 1997; Janson, 1990; Murray *et al.*, 2007; van Noordwijk and van Schaik, 1987). Also, studies suggest that the individual spatial position will influence its predation risk, vigilance levels and even food intake, inlying that certain spatial positions within the group may be more advantageous than others (Hall and Fedigan, 1997; Hirsch, 2007; Janson, 1990; Krause, 1994; Ron *et al.*, 1996). This inequality can lead to the expression of particular spatial behaviours for certain individuals (De Vos and O'Riain, 2010), leading to competition between group members (Ron *et al.*, 1996). Amongst high-ranking females, this results in receiving advantageous commodities such as spatial positioning and food priority. These commodities will reduce the costs and maximize the gains of group-living (Hall and Fedigan, 1997; Janson, 1990; Murray *et al.*, 2007; van Noordwijk and van Schaik, 1987).

Mandrills (*Mandrillus sphinx*) are a clear example of a primate species that exhibits a complex group living structure with a linear hierarchy and strong kin related associations. A social group of mandrills complies with both males and females, yet, less than 2% of the group

is constituted by adult males with other sub-adult and adult males only present during mating season on the periphery of the group (Setchell and Dixson, 2001). The alpha male is the only one that remains continuously associated with the females. Studies have confirmed that males develop a strong linear dominance hierarchy where the chances of any affiliative behaviours occurring between them are low partially since males are often not kin-related (Setchell and Jean Wickings, 2005; Setchell *et al.*, 2006). Females are organized around a matrilineal group (Setchell, 1999), or kin-based female groups, where kin-related females interact with each other more than with non-related members (Bret *et al.*, 2013). Male mandrills compete aggressively with each other for the possibility of mating with a group of females.

Although amongst females, mating competition is not as marked as amongst males, maternal traits are very important for the newborns' survival, possibly affecting the offspring's fitness, influencing growth, development, and physiology (Bernardo, 1996; Mousseau and Fox, 1998). This influence can derive from the mother`s social environment, nutrition, reproductive experience and age [e.g., age-related changes in maternal condition and reproductive strategy (Stearns, 1992)]. One important trait is the mother's hierarchical position (Setchell *et al.*, 2001). Females form a stable linear dominance hierarchy, with daughters ranking immediately below their mothers (Setchell, 2016; Setchell *et al.*, 2008). It has been confirmed, in certain harems and clans, that besides ranking, age is also a very important trait for the fitness of newborns. Both traits (age and rank) have shown to be related to the offspring's somatic growth in both sexes, with higher-ranking or older mothers giving birth to heavier infants (Setchell *et al.*, 2001). Maternally inherited advantages will persist after the weaning period (Setchell *et al.*, 2001) with continuous benefits to descendants, resulting in faster maturation and improved odds of survival to adulthood when compared to the offspring of low-ranking mothers (Setchell and Dixson, 2002; Setchell *et al.*, 2006). Nevertheless, a mother's influence on offspring's fitness is not limited by rank and age. The weight of the mother also seems to have an important impact on the newborn's fitness, with the offspring of a heavier mother presenting a faster maturation (Setchell *et al.*, 2006).

Despite all advantages and disadvantages of social group living, primates remain highly social mammals constantly interacting. Different species may show different types of social interactions with some possibly expressing specific species related social behaviours. Yet, primates share a wide range of social behaviours where grooming has a central role (Henzi and Barrett, 1999) since it allows individuals to stabilize and fortify social bonds over long periods of time (Crockford *et al.*, 2008; Engh *et al.*, 2006; Silk *et al.*, 2012). Grooming is a caregiving behaviour, expressed by physical contact, where one animal touches another animal using its hands, mouth, or other parts of its body (Dunbar, 2010; Newton-Fisher and Kaburu, 2017; Spruijt *et al.*, 1992). This physical interaction resembles scratching, picking, or

rubbing (sometimes may even include licking and nibbling) the outer body surface of the other individual (Dunbar, 2010; Pellis and Pellis, 2010; Spruijt *et al.*, 1992).

1.4.2 Hierarchy steepness and interactions between individuals

It is expected that the social interactions between individuals of the same group may change throughout time based on demographic variables such as changes in age, group size and composition, reproductive condition, resource availability, and social rank (de Waal, 2000; Noe and Hammerstein, 1995).

The study of co-operative interactions in primates requires a deep understanding of the group social dynamics, which are inherently complex and often difficult to measure (Silk, 2002). To understand the frequency and context of co-operative and competitive interactions, one must take into account the degree to which a species is characterized by a rigid or relaxed dominance hierarchy in order to contextualise the social dynamics of the group. In a linear hierarchy, individuals tend to direct their grooming either up the hierarchy, (in an attempt to receive rank-related commodities or create/fortify alliances with more valuable partners, thus strengthening their social rank within the group), or targeting grooming partners of similar social rank (Kurihara, 2016; Xia *et al.*, 2013).

For a deeper understanding of group dynamics, researchers analysed the effects of hierarchy types on the distribution of grooming within group members. When analysing the impact of hierarchy and the intensity of dominance and submissive relationships, one must consider the steepness of the dominance hierarchy. According to de Vries *et al.* (2006, p. 585), the steepness of the dominance hierarchy refers to the "*size of absolute differences between adjacently ranked individuals in their overall success in winning dominance encounters*". If the differences between adjacently ranked individuals are large, the hierarchy is steep/linear, but when they are small, the hierarchy is considered shallow (Flack and de Waal, 2004).

While studying the steepness of the hierarchy, one proposition that has arisen is that with increased steepness, the investment patterns change, directing grooming to be increasingly traded for agonistic support [support against threats such as attacks and pursues from other individuals (Balasubramaniam *et al.*, 2012)]. Alternatively, a decrease in steepness should be followed by a reduction in grooming traded for agonistic support and, instead, it would be more reciprocally traded (Barrett *et al.*, 2002; Barrett *et al.*, 1999).

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1.4.3 Grooming exchange

Individuals express gregariousness via a wide range of social behaviours, frequently exhibiting a wide variety of interactions between dyads and forming social bonds that are commonly maintained over the years (Dunbar, 1988; Silk, 2007). In primates, these relationships are often expressed and maintained via grooming which serves not only as a social interaction mechanism but also as a hygienic procedure (Henzi and Barrett, 1999).

Grooming has shown to be one of the best proxies to analyse how social interactions are regulated in primates. The main reason that makes grooming such an important behaviour is the fact that it helps individuals create and fortify social bonds (Dunbar, 2010).

Despite all the benefits of grooming (social and hygienic), one must keep in mind that grooming interactions also carry costs to the groomer. When engaged in a grooming bout, the groomer spends the time that could be occupied with other activities, namely self-maintenance, eating or sleeping (Cords, 1995; Dunbar and Sharman, 1984). Meanwhile, the groomed individual will receive clear benefits such as stress reduction (Aureli *et al.*, 1999; Keverne *et al.*, 1989) and hygienic benefits (Tanaka and Takefushi, 1993; Zamma, 2002). Being such an important interaction between individuals, grooming has long been used in models of partner choice, exchange, reciprocity (Barrett *et al.*, 1999; Newton-Fisher and Lee, 2011; Saunders and Hausfater, 1988; Schino and Aureli, 2010), and social structure (Brent *et al.*, 2013a; Kanngiesser *et al.*, 2011).

To understand the effects of hierarchy and other group living properties upon social relationships between individuals of a social group, a model to systematically test a theory was created.

1.5 Interactions and exchange of commodities and resources between primates

The biological markets theory [BMT, (Noë and Hammerstein, 1994)] is a model that allows the systematic testing of the theory that social interactions and partner choice is regulated via a marketplace where individuals choose their partners according to the value of the social commodities they can offer (Hammerstein and Noe, 2016). In this model of social interactions, the individual will choose a partner according to the benefits that may receive from such a partnership. In this scenario, the most reciprocal social partners will be favoured for social interactions depending on the current demand and supply of resources or commodities (Barrett *et al.*, 1999; Hammerstein and Noe, 2016). These commodities can

change over time depending on external stressors or necessities, with social tolerance (Barrett *et al.*, 2002), access to food (Fruteau *et al.*, 2009) and access to infants (Henzi and Barrett, 2002) being possible traded commodities. In this model, the core idea for the establishment of collaborative partnerships is that individuals can change their social partners depending on the potential benefits of establishing a different co-operative partnership (Bshary and Noë, 2003).

Following the ideas of the BMT, the longevity of partnerships depends on what commodities are being traded and on the stability of the value of such commodities (Dunayer and Berman, 2016). If the values of the traded commodities are subjected to a high level of oscillations, the value of the partnership itself will be subjected to variation (Dunayer and Berman, 2016). If the value of the traded commodities is relatively stable, the partnership is less likely to change, creating a scenario where long-term trading partnerships can be established (Dunayer and Berman, 2016).

One mechanism that has been studied to explain long-term partnerships is the emotional bookkeeping hypothesis (Aureli and Schaffner, 2002; Schino and Aureli, 2010). This hypothesis argues that traders can maintain a stable and prolonged partnership where single interactions are almost meaningless to compromise the partnership (Aureli and Schaffner, 2002; Hammerstein and Noe, 2016; Schino and Aureli, 2010). In a BMT setting where the emotional bookkeeping mechanism is in place, long-term social interactions are formed from preferred partners that were chosen based not only on their market values but also on the fact that their interactions are regulated and maintained based on the accumulation of emotional experiences that occurred over time (Hammerstein and Noe, 2016).

When analysing the BMT model using grooming as a core interaction for the study of social trading partners, the grooming based BMT or grooming trade model is established (Newton-Fisher and Lee, 2011). This model proposes that if resources can be monopolised in a specific social context, the access to such goods will be directly associated with rank status, with higher-ranking individuals having privileged access. In these contexts, grooming may be used as a bargain "resource" to either receive grooming or rank related commodities. Low ranking individuals will be directing grooming up the hierarchy in exchange for goods or commodities associated with higher-ranking individuals, such as social tolerance (Barrett *et al.*, 1999; Casanova, 2002; Schino, 2001, 2007). However, in communities where resources are equally available to all members, with decreased or absent competition levels, the rank of the individuals will have a diminished influence on the market and, therefore, less influence on the regulation of trades. In this situation, grooming will mostly be reciprocally traded (Barrett *et al.*, 1999). Despite possible oscillations in market values, when analysing the strength and durability of social interactions, the level of reciprocity between partners must be looked at.

Reciprocity levels are correlated with the strength and durability of social bonds (Silk *et al.*, 2004, 2006a; Silk *et al.*, 2006b).

These predictions for the grooming trade model were supported by studies with female baboons, where the exchange of grooming followed the predictions settled by the BMT (Barrett *et al.*, 2002; Barrett and Henzi, 2002; Barrett *et al.*, 1999; Henzi and Barrett, 2002). Also, regarding baboons, females were found not to be very consistent in their social partner choice over time (Barrett and Henzi, 2002; Barrett *et al.*, 1999; Henzi *et al.*, 2009). Despite most studies analysing the grooming trade model focusing on the short-term reciprocal trade of grooming, others brought evidence that, via the emotional bookkeeping mechanism, primates can maintain long-term reciprocal grooming partnerships [capuchin monkeys (Schino *et al.*, 2009) and mandrills (Schino and Pellegrini, 2009)]. Although the studied colony from Schino and Pellegrini (2009) was not a true matrilineal group, female mandrills appear to maintain long-term grooming interactions regulated by the emotional bookkeeping mechanism (Schino and Pellegrini, 2009). Recently, Schino and Lasio (2018) observed female-female competition for access to preferred grooming partners confirming that individuals compete for higher-ranking grooming partners to receive ranking related commodities.

1.6 Robert Seyfarth's Model

Researchers have long recognized the importance of grooming for the social dynamics of primates [see Goosen (1987) for a review]. This behaviour is commonly expressed among Cercopithecidae species and is regarded as a good index of affiliative relations among females (Oki and Maeda, 1973), being defended that when studying the social dynamics in primates, the study of the factors affecting grooming distribution, have the potential to explain unanswered questions about the principles governing primates social structure (Schino, 2001).

The Seyfarth's model (Seyfarth, 1977) is based on the importance of grooming. This model essentially arose from the need to study the factors affecting the distribution of grooming within a social group and the principles responsible for the social organization of the group. Seyfarth's model of social grooming is specially designed for females. It theorizes many aspects of grooming distribution amongst females based on a set of simple organizing principles: (i) attraction to high-ranking individuals (due to "superior value" as potential allies in agonistic contexts); (ii) attraction to kin; and (iii) predisposition to compete for access to the most desired social partners (as time for grooming is thought to be limited). Following Robert

Seyfarth's model, grooming distribution is the result of the interaction between the three mentioned principles [attraction to high-ranking individuals, attraction to kin and competition for access to the most valuable allies (Seyfarth, 1977)]. A high-ranking female may become a valuable partner within a social group since she is capable of delivering high-ranking related commodities. This means that, with grooming being exchanged by a range of commodities and with high-ranking females providing agonistic support and other commodities more effectively (Schino, 2007), high ranking females are likely to be more valuable and desired as trading partners or, more precisely, as grooming partners (Schino and Aureli, 2008b). With the group members directing their attention and grooming time to higher-ranking females, and with higher-ranking individuals having limited availability for grooming exchange, it is expected that lower-ranking females must compete for such partnerships. In such competition, when compared to higher-ranking females, lower-ranking ones are hypothesised to be less successful in accessing higher-ranking grooming partners (Schino, 2001).

1.7 Hypothesis and predictions

1.7.1 Hypothesis and prediction's introduction

The study of primates' social behaviour requires deep knowledge about the specific species ethogram and social structure. Some behaviours may even vary across the life cycle of an individual. Despite the current knowledge available for baboons and other Cercopithecidae species, the understanding of social behaviour in mandrills remains scarce.

The mandrill is a complex social species with females organized in kin-based groups, in a highly complex and dynamic social structure where a high number of social relations can be seen, presenting researchers with the opportunity to test grooming models for cercopithecoids (Abernethy *et al.*, 2002). Our targeted mandrill colony is a true matrilineal group, a rare feature seldom observed in captive colonies (but commonly observed in the wild). Thus, this work also represents an opportunity to look at the social behaviour of a true matrilineal group, especially for the study of the relation between grooming behaviour and social rank (dominance hierarchy) which allows the investigation of social interactions of a mandrill group that mimics the structure expected in the wild (on a small scale) which data is scarce and difficult to obtain (Setchell, 2016)

Although grooming is well studied in Cercopithecoids, especially in baboons (Barrett *et al.*, 1999; Saunders and Hausfater, 1988; Schino *et al.*, 2003; Zamma, 2002), knowledge

on grooming interactions, fitness consequences, and how grooming is affected by other factors such as kinship and status for mandrills remains understudy (Abernethy *et al.*, 2002).

In this study, I intend to understand if grooming interactions amongst females of the studied mandrill colony follow the predictions established by the grooming trade model. First, I want to study and describe the two central components in the study of grooming interaction: partner choice, and the use of grooming as a tradable "resource" not only for itself but also for other commodities in a marketplace. To understand these components, I established a set of hypotheses based on current knowledge on the regulation of grooming in mandrills and the BMT.

Some of these predictions were analysed in a previous study conducted on the same colony, over two independent periods (Pereira *et al.*, 2019). However, social life is dynamic, and, as shown by Pereira *et al.* (2019), there are important differences in the social behaviour of the colony in the two observation periods. Because it is important to understand what drives variation in social behaviour, it is relevant to test hypotheses in new independent periods. This study can help us not only to understand the effects of time in the grooming social network but also to understand the consequences of changes regarding the number of individuals (demographic changes) and the growth and maturation of juveniles. In this dissertation, I established a set of predictions that were assessed through statistical analysis.

1.7.2 Social Rank

Based on the results of Pereira *et al.* (2019) I assume that grooming is traded in a marketplace system, with higher-ranking individuals trading rank-related commodities (e.g., social tolerance). With the trade of rank-related commodities for grooming, the frequency at which an individual receives grooming should be related to its hierarchy ranking status. With rank-related commodities being traded in a marketplace and with limited goods being monopolized by higher-ranking individuals (Barrett *et al.*, 1999), higher-ranking colony members will be able to trade rank-related commodities for grooming [e.g., Seyfarth (1977) and Schino (2001) for a meta-analysis on Ceboidea and Cercopithecoidea- Kaburu and Newton-Fisher (2015) for chimpanzees- and Pereira *et al.* (2019) and Schino and Lasio (2018) for mandrills]. There is also evidence that in a marketplace, individuals are more likely to direct grooming to higher-ranking individuals when the dominance hierarchy is steeper/unbalance (Schino and Aureli, 2008a). Limited resources such as food or space must intensify these effects increasing the values of higher-ranking females even more. Following this chain of thoughts, I predict that higher-ranking females will receive more grooming than lower-ranking

females (H_1) and I also expect females to direct their grooming up the hierarchy (H_2) [e.g., Seyfarth (1977) and Schino (2001) for a meta-analysis on Ceboidea and Cercopithecoidea- Kaburu and Newton-Fisher (2015) for chimpanzees- and Pereira *et al.* (2019) and Schino and Lasio (2018) for mandrills].

Given that rank defines access to rank-related benefits, it is predictable that individuals with similar ranking status exchange more similar commodities with each other (Barrett *et al.*, 1999). Following this prediction, I expect individuals to groom others of similar rank (closer in the hierarchy status) more often (H_3).

1.7.3 Grooming reciprocity

It is expected that females trade grooming for other benefits. However, it can also be hypothesized that (H_4), even if grooming is exchanged for other benefits, it remains a valuable commodity on its own, resulting in reciprocal interactions between the individuals of the studied colony.

1.7.4 Partner choice for grooming trade

It is expected that females engage in grooming interactions with only a few specific individuals, maintaining their partner choice across the observation period (H_5). This prediction follows the results of prior research on cercopithecoids (Brent *et al.*, 2011; Silk *et al.*, 2012; Silk *et al.*, 2010), and later confirmed in mandrills by Pereira *et al.* (2019).

1.7.5 Tolerance

In captivity enclosures, there are likely fewer stressors than in the wild (although the lack of opportunities to escape attacks by group members may constitute an additional stress factor). It seems likely that, in captivity, food competition between individuals is lower, but space may be a limiting factor that results in intragroup competition. If grooming is traded for rank-related commodities, social tolerance (to avoid or mitigate aggression and supplants), is likely to be a valuable resource. Therefore, I expect (H_6) that individuals that groom each other more frequently are more tolerant to each other's presence, and are thus less likely to engage in agonistic behaviours with each other (Kaburu and Newton-Fisher, 2015; Pereira *et al.*, 2019; Schino, 2001; Schino and Lasio, 2018; Seyfarth, 1977).

2. Material and methods

2.1 The mandrill

2.1.1 Habitat and species distribution

Mandrills (*Mandrillus sphinx*) are terrestrial cercopithecine primates native to the moist evergreen rainforest of central west Africa, south of the Sanaga River (Cameroon), dispersing into the mainland Equatorial Guinea, occupying part of southern Gabon and south-western Republic of Congo into the Kouilou River, and down until the Congo River. Limiting its distribution to the east stands the Ivindo and Agooué Rivers in Gabon (Allam *et al.*, 2016; Fay, 1989). The north-western limit of their range in Cameroon appears to be in Dja Biosphere Reserve, where mandrills have been recorded through the use of camera traps (Bata *et al.*, 2017). The use of camera traps has also enabled the record of mandrills at the source of the Agooué, extending the species' range into the Batéké Plateaux National Park of Gabon (Abernethy and Maisels, 2019). Until now, there seems to be no records of mandrill's presence in south-east Cameroon or east of the Congo River (Figure 1). These natural barriers separate the species range into two distinct populations, one in Cameroon, Equatorial Guinea and northern Gabon, and the other in southern Gabon and Congo (Telfer *et al.*, 2003). As a result of the limited geographical distribution, hunting pressure and habitat loss caused by humans, IUCN recognized *M. sphinx* as Near-Threatened (Baillie and Groombridge, 1996; Oates, 1996) and even changed his classification status more recently to Endangered (Abernethy and Maisels, 2019).

Mandrills are morphologically similar to baboons (*Papio* spp. and *Theropithecus gelada*) and, traditionally, both mandrills and drills (*Mandrillus leucophaus*) were considered to be "forest baboons". Today is well known that mandrills and drills are genetically closer to *Cercocebus mangabeys* than they are to the genus *Papio* (Disotell, 1996; Fleagle and McGraw, 1999). Like baboons, mandrills are mainly ground dwellers, omnivorous, and very social animals.

Unlike other primates, mandrills are especially hard to study in the wild. As a consequence, there is still very little knowledge about the species. Until today, only a small number of studies have been conducted on wild mandrill populations, with researchers agreeing that finding and following mandrills for more than a few days is an extremely difficult

task (Harrison, 1988; Hoshino, 1985; Hoshino *et al.*, 1984; Jouventin, 1975; Lahm, 1985; Lahm, 1986; Rogers *et al.*, 1996; Sabater Pi, 1972).
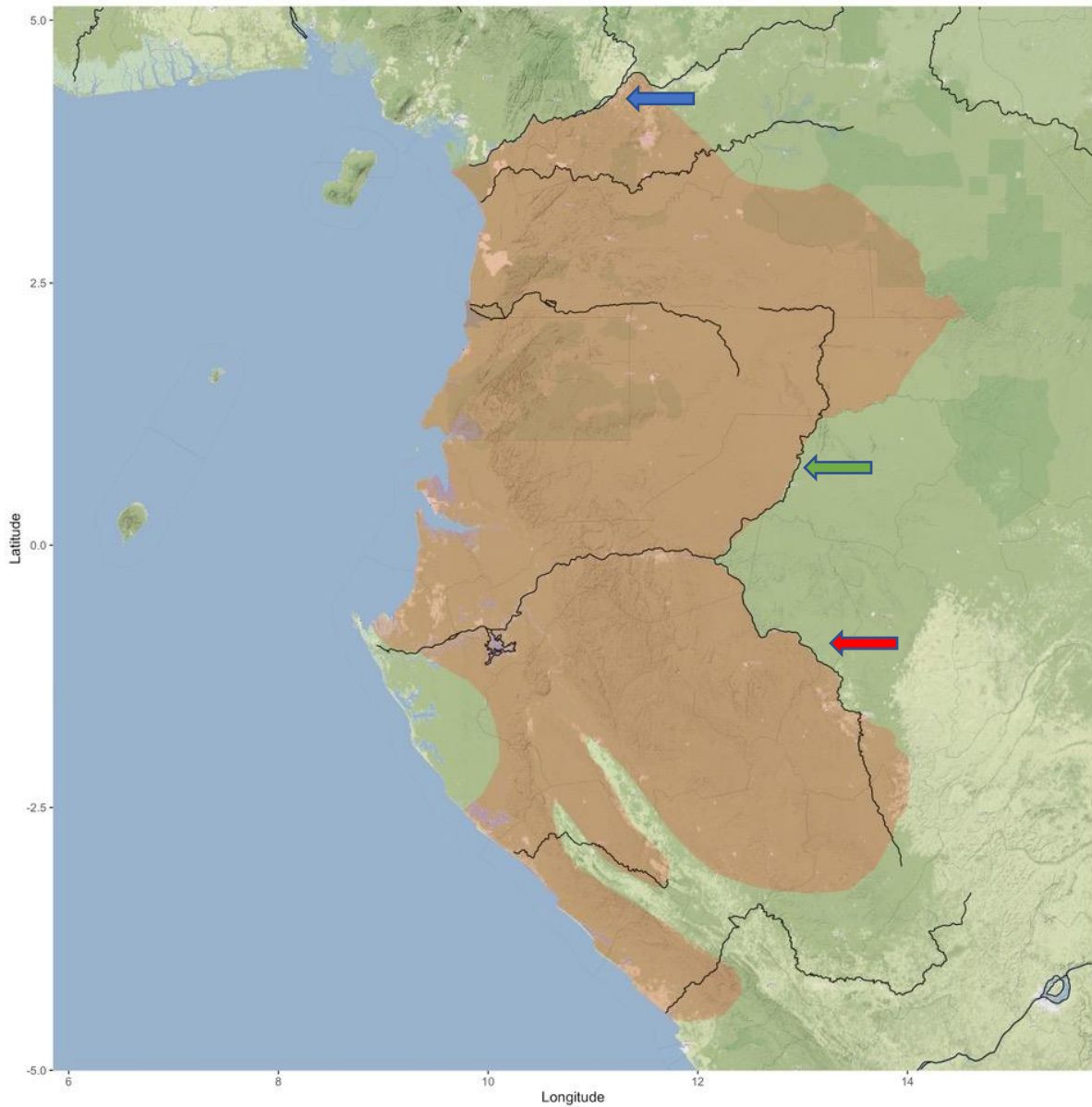
Figure 1: Mandrill geographical distribution (range, as suggested by IUCN, shown as red shaded area; Sanaga river marked by the blue arrow, Agooue river marked by the red arrow and the Ivindo river marked with a green arrow).

2.1.2 Morphology, sexual dimorphism and dichromatism

Mandrills are one of the most fascinating examples of sexual selection in the mammal world. The unique set of armaments and ornaments has long converted the species into a classic example for the evolution of sexual selection in primates. Since Darwin first proposed his original theory of sexual selection (Darwin, 1871b), the understanding of the process and its drivers have expanded. But that doesn't change the fact that, already in 1871, Darwin was astonished by the male mandrill portrait, stating that "*no other member in the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill*" (Darwin, 1871a, p. 292). Darwin's original theory of sexual selection was developed to integrate exaggerated male traits such as the peacock`s tail, the elk's antlers or the glaring colour of the male mandrill (Darwin, 1871a, p. 293). Although these exaggerated traits are not required for the copulation process itself or for survival (and may even pose a challenge by increasing the exposure to possible predators), Darwin theorised that such traits would increase the individual mating success and nature would favour them even with the cost of a reduction in survival (Darwin, 1871b). Following Darwin's theory, reproductive advantages can either be achieved by intrasexual competition or by mate preferences, thus explaining the development of apparently maladaptive secondary sexual characteristics (Darwin, 1871b).

Like most polygenic species, the variance in the reproductive output in mandrills is far greater amongst males than females. Only a reduced number of males can hold and protect a group of females for reproductive purposes, resulting in a large variance in reproductive success in males. Unlike males, most females end up producing offspring while only one in three males is able to sire offspring (Setchell *et al.*, 2005b).

When compared to females, males can usually sire a greater number of offspring. During the full extent of their lifetime, a single male can produce a far greater number of offspring (maximum observed of 41) than a female [maximum observed of 17 (the influence of captivity is unclear in these results, due to the absence of predators and food provision in captivity - see (Setchell *et al.*, 2005b)]. This variation in reproductive success results in an intensive male-male competition to sire offspring. This competition results in the selection for larger male body size [Figure 2-3; (Leigh, 1992; Shea, 1986)], and large canines with those from males reaching up to 5 cm in height [Figure 4; (Leigh *et al.*, 2008)], being longer than those of any other primate (Plavcan and van Schaik, 1992). Such long canines probably result from a process of intrasexual selection, being used as weapons during male to male combat and as an advertisement of the male capability, thus avoiding unnecessary combat (Plavcan and van Schaik, 1992). As sexual selection is not as strong in females, sexual dimorphism

arose. As such, sexual and natural selection shaped this primate into the largest Cercopithecidae [Figure 2 and 3; (Setchell, 2016; Setchell *et al.*, 2006)], presenting a strong sexual dimorphism, with the difference in size being a very noticeable dimorphic trait, where males weighting an average of 31Kg are conspicuously larger, with a mass 3.4 times more than females [Figure 2; (Setchell *et al.*, 2001)]. Together with extraordinary colouration (sexual dichromatism), these traits make mandrills one of the most sexually dimorphic primates [Figures 3 and 5; (Setchell and Dixson, 2001)].

Figure 2: Male mandrill (in the center) and an oestrous female (left).

Males are easily recognizable due to their characteristic facial colouration (Figures 2 and 3) which seems to stem from the action of sexual selection (Setchell, 2005; Setchell *et al.*, 2009). This facial coloration consists of a bright red stripe which blazes from between the mandrill`s close-set eyes up to the nose, enclosed by ribbed blue stripes in the sides (Figures 3 and 5)

Figure 3: Dominant male mandrill.

Apart from facial colouration, coloured genitalia also seems to be an important character calling the female's attention (Setchell, 2005). Both males and females present long limbs, proportional to their compact bodies, with a brownish olive-coloured fur coat and a paler undercoat, white tufts, red hair patches above the eyes, a yellow beard (Figure 3) and a stubby and uptight tail (Figure 5).

In terms of longevity, the average life span in captivity for members of the genus *Mandrillus* stands between thirty and forty years (Weigl, 2005, p. 214). Under semi-free-ranging conditions at the Centre International de Recherce Médicales, Franceville (CIRMF), Gabon, males average lifespan is fourteen years, while females usually live for at least twenty-five years (Setchell *et al.*, 2005a).

Figure 4: Dominant male mandrill threatening submissive male (exhibiting canines).

Figure 5: Submissive male mandrill (named Mapendo), with a clearly visible short tail.

2.1.3 Mandrill socio-ecology

With a home range as large as 81 km^2 (White *et al.*, 2010), mandrills are known to be able to form considerable, possibly non-nested (Hongo, 2014), aggregations, called "hordes", of hundreds of individuals (Harrison, 1988; Jouventin, 1975). Although the composition of such groups is still subject of debate, Abernethy *et al.* (2002) reported that mandrill societies could form a stable social unit not divided into any subgroup (or at least rarely divided) comprising

between 1-17 adult males, with the number of mature males fluctuating seasonally according to the number of females displaying sexual tumescence. From such observations, Abernethy and collaborators hypothesized that mandrills live in a female-led society where males are not resident members, but migrants who enter hordes according to the female seasonal cycles.

Despite the lack of knowledge regarding group compositions and structure and the social behaviour of the species, the mandrill's diet is well known. As a result of many indirect studies (via the identification of food remains and faecal analysis), today is known that this primate is omnivorous, with a flexible diet, eating insects, leaves and pith from monocotyledonous plants and fruits (Hoshino, 1985; Jouventin, 1975; Lahm, 1986). Both the diet (dependent on patchy food sources) and the large number of feeding resources necessary to fulfil the need of the horde could be a possible explanation for their home range size. Yet, it remains unknown if large mandrill groups are a regular occurrence in all regions or if they are a product of specific regional or seasonal events.

Despite all threats to mandrill populations, there are still a few places with low-human pressure in the African continent. One very important country for the conservation and study of the species is Gabon. The existence of areas with low or even non-existent hunting pressure from humans provided a safe place for mandrills (Harrison, 1988; McShane, 1990; Tutin and Fernandez, 1987). In 1983, in the Lopé Reserve, the Station d'Estudes des Gorilles et Chimpanzés (SEGC) was established. Since the establishment of the SEGC, it was possible to better understand some of the species' behaviour and group structure. Mandrills passed through the gallery forests and the savanna-forest edge in large numbers during the annual major dry season with an average group size of 150 and, occasionally, with over 400 individuals (Harrison, 1988; White, 1994; White *et al.*, 1995).

At the CIRMF, data has been obtained relative to the ecology, behaviour and social organization of the species (Norris, 1988; Wickings *et al.*, 1993; Wickings and Dixson, 1992a, 1992b). One particularly interesting study has shown the existence of two morphological variants of male mandrills (brightly coloured, or "fatted", and paler, or "non-fatted") with different rates of reproductive success (Wickings *et al.*, 1993). The study of such variants may be important to explain the social organization of the species.

2.2 Studied colony and captivity enclosure

In the present work, I describe and analyse social behaviours in a mandrill colony, namely grooming, propinquity and dominance interactions via focal sampling. Data was collected during the year 2020 but, I will also resort to data collected in 2016 and 2018, from the same colony [first (2016) and second (2018) independent periods from Pereira *et al.* (2019)], for the discussion section of this thesis.

The studied colony was housed in the Badoca Safari Park, Setúbal, Portugal [38º02'26.5'N8º44'35.8'W; (Figure 6)] and consisted of 12 individuals. Information regarding the family tree (Figure 7), sex, age, birthplace (Table 1) and reproductive status was provided by the Veterinarian Department of the Badoca Safari Park. The focus of the study were the 6 females (Table 1), who formed a single matriline (Figure 7). One of the advantages of the park comes from the fact that the animals live in a captive setting where variables are controlled (which does not happen in the wild). The individuals of the colony were fully habituated to the presence of visitors and observers.

Figure 6: Island- outdoor enclosure of the Badoca Safari Park mandrill colony (internal area of 1673.55 m^2)
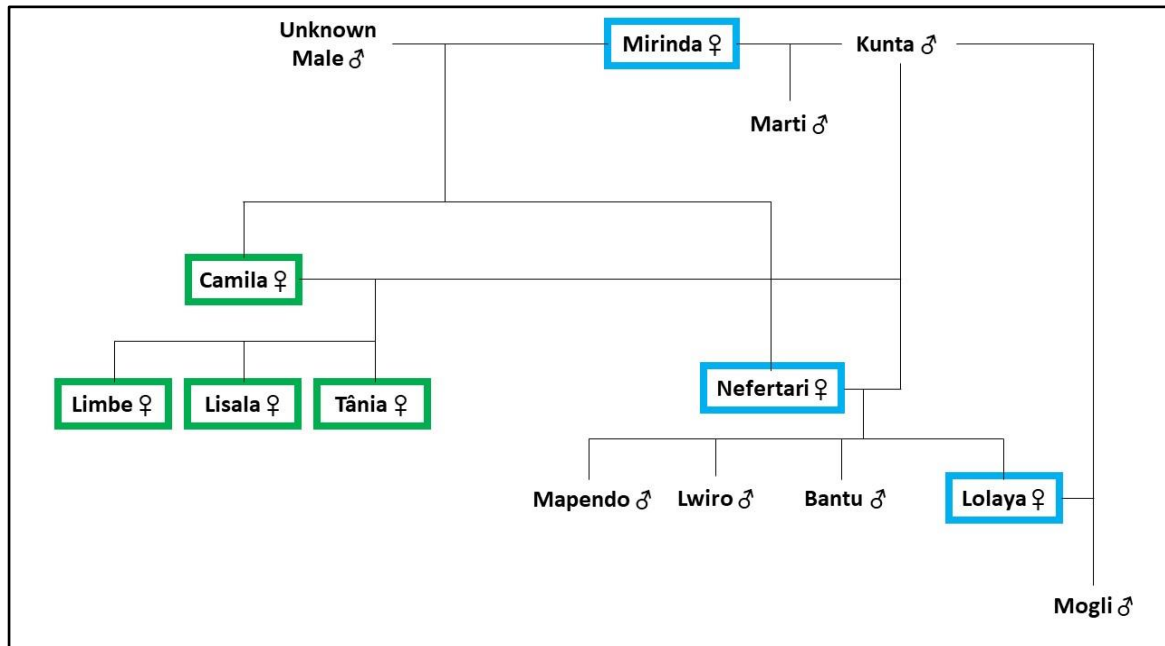
Figure 7: Family tree of the Badoca Safari Park mandrill colony. The most dominant females are presented in green while the most submissive females are presented in blue.

Table 1: Female mandrill colony members in Badoca Safari Park.

Individual	Sex	Age (2016)	Age (2018)	Age (2020)	Birthplace
Mirinda	F	20.9	22.6	25.2	Zoologicka Zaharada Usti na Labem (Czech Republic)
Nefertari	F	15.7	17.4	Deceased	Barcelona Zoo (Spain)
Camila	F	13.9	15.6	18.3	Barcelona Zoo (Spain)
Limbe	F	5.2	6.8	9.5	Barcelona Zoo (Spain)
Lisala	F	3.7	5.3	8.1	Barcelona Zoo (Spain)
Lolaya	F	3.6	5.3	8.0	Barcelona Zoo (Spain)
Tânia	F	2.3	4.1	6.7	Barcelona Zoo (Spain)

Regarding ethical concerns, permission to conduct this study was provided by the Park`s Animal Department, and because data collection only implied the observation of the colony members with no direct contact, no further permissions were required. The study protocol was elaborated according to the European law on human care and the use of

laboratory animals and the ASAB guideline for the observation of animals (ASAB, 2018) and was conducted without intervening or changing the daily primate management programme and timetable. Precautions regarding the olfactive cues were taken, namely the use of the same hygiene products by the observer (Martin and Bateson, 2007). During each data collection period, all focal females were under contraception by a gonadotrophin-releasing hormone agonist, which is believed to have no direct impact on the social interactions of Cercopithecidae species (EGZAC, 2014).

Regarding changes in the composition of the colony, in 2016, Bantu was dependent on Nefertari for milk and transport. In 2018, the number of focal females increased to 7 with the maturation of Tania and the total number of colony members increased to 13 with the birth of Mogli, 15 weeks after the 2016 data collection period. This indicates that, during period one, the female Lolaya was pregnant despite being under contraception.

Regarding the daily schedule of the colony, food was distributed every morning in the outdoor installations (before releasing the group from their night indoor installations). The distributed food was diverse: vegetables, fruit and seeds were always included. Before returning to the indoor installations, fruit, vegetables and seeds were also available to ensure that all individuals could be fed after returning to the indoor installations. Water was available *ad libitum*. All data for this study were collected during the day, in the outdoor enclosure, which has approximately 1674 m^2 of available space (Figure 6). The enclosure was environmentally enriched with natural elements such as bushes and trees and artificial elements such as wood man-made structures. The captive enclosure provides some privacy from the visitants and protection from the weather. Table 1 shows the colony composition (females) during the focal sampling over all periods of data collected from the colony.

2.3 Habituation period

To ensure the reliability of the data collected for this thesis, i.e., to make sure the data were not biased by human novelty or by data collection inexperience, a habituation period was conducted. In this period, the observer remained in the presence of the mandrills, gathering information on the colony and identifying distinctive features of each individual. During the habituation period, the observer also recognized the patterns of behaviour that constitute the mandrill ethogram (Annex C). Behavioural data collected before conducting the observer reliability tests were discarded (Martin and Bateson, 2007). The reliability test consisted of randomly selecting a focal individual that was video recorded for 15 minutes. This video record was observed and behaviours were registered four times with a two days gap between each

registry. Comparisons were conducted by computing an adapted concordance index (CI= $\frac{A}{A+D}$ ×100) where A is the number of agreements and D is the number of disagreements. When the CI reached 95% (Martin and Bateson, 2007), the data collection period officially started (with data collected prior to the 95% index being discarded). This procedure ensured consistency regarding data collection by the observer.

2.4 Sampling protocol

2.4.1 *Ad libitum* sampling

Ad libitum sampling was used during the habituation period to record the distinctive features of each individual and the ethogram of the species (with a strong emphasis on social behaviour). This type of sampling also allows for the observer to record episodes that are considered important (Martin and Bateson, 2007).

2.4.2 Focal sampling

All data were collected through focal samples (Altmann, 1974; Martin and Bateson, 2007). Focal sampling is the most appropriate method to collect behavioural data, in particular social data (Martin and Bateson, 2007). I conducted focal samples on all the female colony members. As previous data on the same colony (2016 and 2018) followed a similar sampling protocol, I was able to compare and discuss results between the three sampling seasons. Focal samples were registered in a proper "daily-sheet" (Table A17), where several details about the observed behaviours were recorded.

All colony members were recorded a similar number of times throughout the day to keep the numbers of samples as balanced as possible. This way, the identity of all actors (recipient and initiator), behaviours duration and the type of behaviour were registered. Focal samples lasted for 15 minutes and were distributed equally amongst females with the order of focal individuals being randomly decided for the first day (a list was initially computed with random focal individuals). After the first day, focal sampling would start with the next focal on the list, and so on. This procedure allowed me to avoid time-specific skews in observation by changing the focal identity through the different hours of the day.

2.5 Additional protocol information

For this dissertation, data were collected during a two-month period (2020). A total of 415 focal samples were recorded for the 6 females, totalling 103.75 hours of data [focal samples from Pereira *et al.* (2019) were: 2016 = 384 focals (96 hours), 2018 = 294 (73,5 hours)]. Table 2 shows, the number of focal samples per female per time-block.

Table 2: Table of focal samples per time-blocks/shifts, per individual.

Time-Block / Individual	Morning	Afternoon	Total
Mirinda	29	40	69
Camila	29	40	69
Limbe	31	38	69
Lisala	30	39	69
Lolaya	27	43	70
Tânia	31	38	69
Total	177	238	415

I registered the time each female spent in proximity of each other. When registering proximity between individuals, I distinguished two types of proximity: "proximity" and "arms reach" (AR). While AR meant that individuals were spatially located within arm's reach of each other, proximity meant that individuals were within 3-4 meters from each other. I also distinguished AR and 'AR while eating' (ARE), registering any individual as being at ARE when the individual was at AR of the focal while the focal was eating, chewing, or searching for food.

In terms of climate, because the colony was housed in a semi-controlled environment, I do not expect seasonality to influence the behaviour of the colony members, apart from the increased usage and possible competition for shading areas, when the sunlight was strong, or artificial structures, when it was raining.

To help the data collection process, I used a 10 x 20 binocular, provided by the park. I would indicate all observed behaviours and information regarding the time of occurrence while the field assistant was responsible for the writing of such data in paper. A voice recording device was used to ensure that all information observed was correctly registered in the paper. Data were later transcribed into digital format by both the author and the field assistant.

2.6 Data analysis

The social dynamic of the colony was mainly characterized through grooming interactions (Figures 8 and 9) and other behaviours such as supplants and avoidances. I organized the total duration of grooming that each individual spent grooming another [measurement of grooming effort as suggested by (Newton-Fisher and Lee, 2011)] creating a non-symmetric square matrix (Table 3). For descriptive analysis, I also presented grooming distribution patterns over a set of graphics (Figures 10, 11 and 12). To help visualize the patterns of grooming up the hierarchy I calculated the total grooming effort directed up the hierarchy by each female (Figure 12)[1].
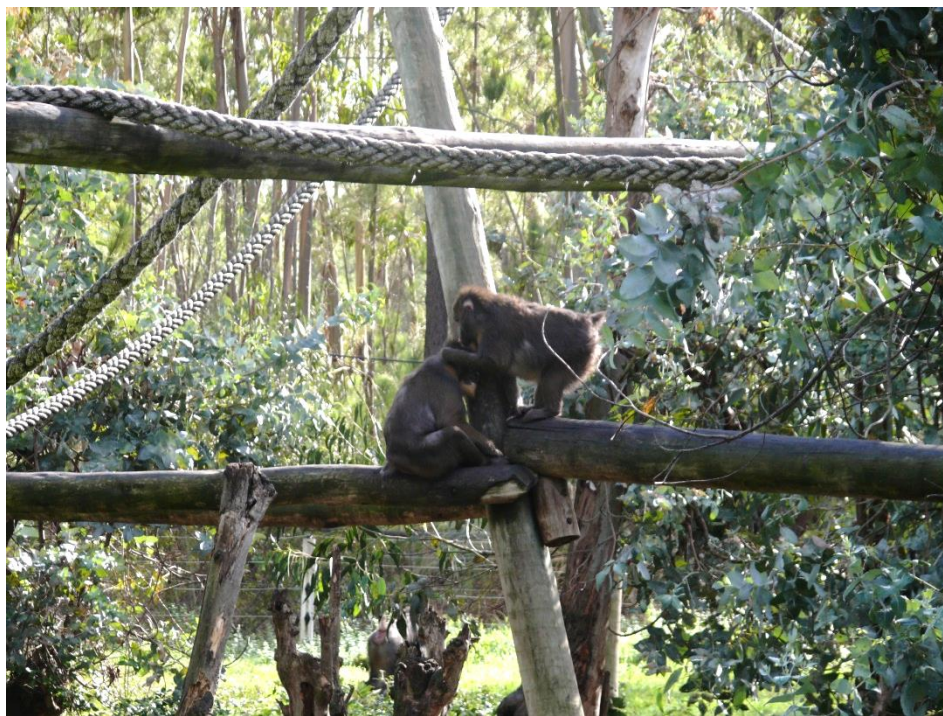
Figure 8: Social grooming between two mandrills (Camila grooming Lisala).

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[1] Similar graphics can be observed for 2016 and 2018 data in appendix A

Figure 9: Social grooming between two mandrills (Lolaya grooming Mogli).

To establish the social hierarchy between the focal females, I calculated each individual's average Dominance index [DI, Hemelrijk *et al.* (2005)] based on the outcome (wins/loses) of supplants and avoidance interactions. I only used supplants and avoidances to build the hierarchy. Supplants and avoidances allow for unambiguous observation of dominance display, which is not always the case with aggressive and submissive interactions (Hinde, 1978).

For the analysis of the hierarchy steepness, a cardinal rank measure was used (Flack and de Waal, 2004). One way of obtaining the cardinal rank is through the calculation of David's score. David's score has shown potential to be used as a tool to analyse how the hierarchy status of individuals affects the distribution of grooming within the group [see Xia *et al.* (2012)].

There are two main methods to obtain David's score. The first allows the calculation of David's score values through the dyadic proportion of wins from agonistic interactions [$P_{(ij)}$]. Despite its merits, this method was found to be inadequate for some statistical analyses. David (1988) noted that the P_{ij} values are not well suited when the number of interactions between dyads greatly differs. Here I used the most recent method from de Vries *et al.* (2006), an improved version of de Vries (1998)[2].

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[2] For a detailed description and analysis of the method, read de Vries et al. (1998) and de Vries et al., (2006).

Since David's scores, for 2016 and 2018, were unavailable, in order to compare the hierarchy steepness of 2020 (this dissertation results) with that of 2016 and 2018 (Pereira *et al.* (2019), I calculated David's score values for the three observation periods (2016, 2018 and 2020) based in a matrix of agonistic interactions (supplants and avoidances). David's scores were obtained in R v4.0.4 (R Core Team, 2021), using the R package EloRating v0.46.11 (Neumann and Kulik, 2020). The function used to calculate David's score values derives from the work of de Vries and collaborators (de Vries *et al.*, 2006), where the most recent method to calculate and normalize David's score values was originally reported. After normalizing the values for all periods, I calculated the slope of the plots for 2016, 2018 and 2020 (de Vries *et al.*, 2006).

When analysing social data, data dependency is inevitable and, consequently, tests conducted with social data share a common statistical problem. For example, for individual A to have five social partners, it means that all those five partners have at least one social partner (the individual A). That means that, in statistical terms, the number of social partners of the individual A is not independent of the number of partners of the others individuals [the five social partners of individual A (this problem applies to all social and dyadic analyses)]. The dependency present in this type of data breaks the fundamental statistical assumption of independence (Croft *et al.*, 2011; Hemelrijk, 1990b; Weiss *et al.*, 2020). To address the problem of data dependency, several statistical tools have been developed, primarily in the social sciences. These tools are based on permutation techniques that allow the user to test the hypothesis in the presence of dependent data points (Croft *et al.*, 2011; Hemelrijk, 1990b; Weiss *et al.*, 2020). In this study, I used the tau K_r test, which employs a permutation approach (Hemelrijk, 1990a). This procedure has been widely used in the study of social grooming in primates, for example, to calculate reciprocity in primates grooming (Hemelrijk, 1990b; Newton-Fisher and Lee, 2011; Pereira *et al.*, 2019).

To test the hypothesis that higher-ranking females receive more grooming than lower-ranking females (H1), I calculated the total amount of grooming each female received (G_{rec}), and the total amount of grooming each female gave (G_{giv}). To avoid division by zero, I divided the grooming received by the grooming given (G_{rec}/G_{giv}). Through Spearman's rank correlation, I tried to see an association between grooming (G_{rec}/G_{giv}) and the female's dominance rank (Kaburu and Newton-Fisher, 2015).

To investigate if grooming was directed up the hierarchy (H$_2$), I calculated the expected and the observed proportion of grooming directed to higher-ranking females for each female and tested if there was a significant difference between the values (Kaburu and Newton-Fisher, 2013; Newton-Fisher and Lee, 2011). Following Newton-Fisher and Lee (2011) and Kaburu and Newton-Fisher (2015), I calculated the expected proportion of grooming directed

up the hierarchy by taking the total amount of grooming performed by each female and multiplying it by the proportion of females with higher hierarchy status based on their DI scores. Afterwards, I subtracted the expected values from the observed values for each female and analysed if the difference between both values was significantly different from zero using the Wilcoxon signed-rank test in the SPSS program.

To test if dyads closer in ranking status were more reciprocal (H_3), I calculated an index of reciprocity for each dyad, as proposed by Newton-Fisher and Lee (2011) and Kaburu and Newton-Fisher (2015). For this test, I adopted the reciprocal grooming index from Mitani (2009) which is a rescaled version of the Nishida (1988) index. Following the proposal by both Newton-Fisher and Lee (2011) and Pereira *et al.* (2019), I labelled the grooming reciprocity index as gRI. In the computation of gRI [1-|gAB/(gAB+gBA) -gBA/(gAB+gBA)|], gAB is the amount of time, in seconds, that individual A spent grooming the individual B and gBA is the time, in seconds, the individual B spent grooming individual A. The sum of gAB and gBA is the amount of time that individuals A and B spent grooming each other. The index gRI varies from 0 (grooming trade is unidirectional - unidirectional partnership) to 1 (grooming is perfectly reciprocal). After calculating the gRI for each dyad, I constructed a symmetric matrix and used the tau K_r test (Hemelrijk, 1990a) to correlate it with a matrix of each dyad's social rank distance (the rank difference of the hierarchical ordinal position). A negative correlation allowed me to verify if higher values of gRI are correlated with lower rank distances. For H_4, to look for evidence of grooming reciprocity across dyads, I used the Tau K_r test to correlate matrices of given and received grooming (Hemelrijk, 1990a).

To test if the females in the colony chose only a few specific partners to exchange grooming (H_5), I started by using the standardised Shannon Weaver index (Henzi *et al.*, 1997; Kaburu and Newton-Fisher, 2015; Newton-Fisher and Lee, 2011; Silk *et al.*, 1999) to calculate the diversity of grooming partners for each female. In the calculation of the Shannon Weaver index [H''=(pi × ln pi+pi+1 × ln pi+1+pi+2 × ln pi+2+…+pn × ln pn)/(ln n-1)], n is the number of mature females of the colony and p is the proportion of grooming frequency that a female-directed to each of the other females. The Shannon Weaver index values can range from 0 (all grooming was focused on a single partner) to 1 (given grooming was equally distributed across all potential grooming partners). The diversity of grooming partners can help us understand individual variation in grooming effort (partner focus) for their partner choice when the number of available partners is the same for every female colony member (Newton-Fisher and Lee, 2011). To test if individuals maintained their grooming partners across time periods (H_5), I compared the data from 2018 (Pereira *et al.*, 2019) with the data I collected for this dissertation. I constructed a binary matrix of partnerships for each period. Following Pereira *et al.* (2019), I used a binary matrix (rather than a weighted matrix with grooming time or the

number of grooming episodes) because this hypothesis refers only to the maintenance of partnerships, not to whether the quality of partnerships remained the same. In the binary matrix, for each female, I attributed the value "1" to all groomed females and "0" to the females that were never groomed. Afterwards, I correlated this binary matrix with the 2018 binary matrix using the tau K_r matrix correlation test (Hemelrijk, 1990a). In this computation, I included only the females that were present in both periods (i.e., I excluded Nefertari, which was no longer part of the colony). The main goal of this test was to understand if pre-existing partnerships were maintained across periods.

To test if grooming was traded for social tolerance (H_6), I computed the correlation between a directed grooming matrix with a matrix containing the number of supplants and avoidances. For this correlation, I, again, used the tau K_r test (Hemelrijk, 1990a). Apart from the correlation between grooming and agonistic interactions, I also computed the correlation between the symmetric matrix of total grooming traded between dyads with a symmetric matrix of the ARE time, using the tau K_r test.

All statistical calculations (matrix permutation tests) using tau K_r tests as well as the average DI were calculated using the Matrixtester add-in for Microsoft Excel (Microsoft, Redmond, WA, USA). All the reported probabilities are two-tailed.

3. Results

3.1 Grooming distribution

A total of 20,638 seconds of grooming behaviour between dyads (distributed across 387 bouts) was registered during focal sampling. From the focal samples, I constructed a grooming matrix (Table 3).

Table 3: Grooming matrix for 2020 (in seconds).

Groomed / Groomer	Camila	Tânia	Lisala	Limbe	Lolaya	Mirinda
Camila	0	8391	1027	231	0	0
Tânia	800	0	4	0	251	0
Lisala	3834	772	0	0	15	0
Limbe	1070	0	224	0	0	0
Lolaya	32	3583	17	0	0	0
Mirinda	0	0	0	0	0	0

By analysing grooming distribution, the following results can be observed: Mirinda did not trade any grooming. Thus, excluding Mirinda, Camila was the female who gave most grooming and Tânia was the female who gave less grooming (Figure 10). The female receiving most grooming was Tânia and once again, excluding Mirinda, the female receiving less grooming was Limbe (Figure 11).

Regarding grooming up the hierarchy, Camila was the most dominant female, thus unable to direct grooming up the hierarchy. Lisala was the female who gave most grooming up the hierarchy while Tânia (excluding Mirinda) was the female who gave less grooming up the hierarchy (Figure 12). Besides grooming distribution, the matrices presenting the time of proximity, AR and ARE (Tables 4-6) show us that Tânia and Lisala were the females spending most time in proximity. Tânia and Camila were the females spending more time at AR and ARE and Mirinda was not observed at AR or ARE with any other female.

Through the grooming partnerships (a grooming partnership is established when a female gives or receives grooming for any amount of time) I can observe that all females, with the exception of Mirinda, which did not give or receive any grooming, groomed between 2 and

3 females, with all females possessing one partner to which they gave more than 70% of their grooming (Table 7).
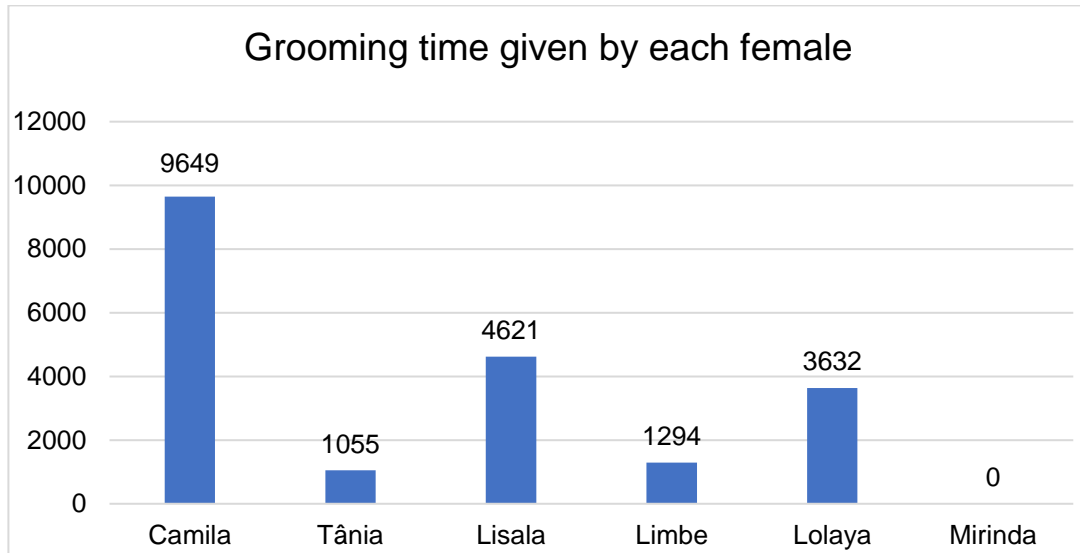
Figure 10: Given grooming time (in seconds) by each female.
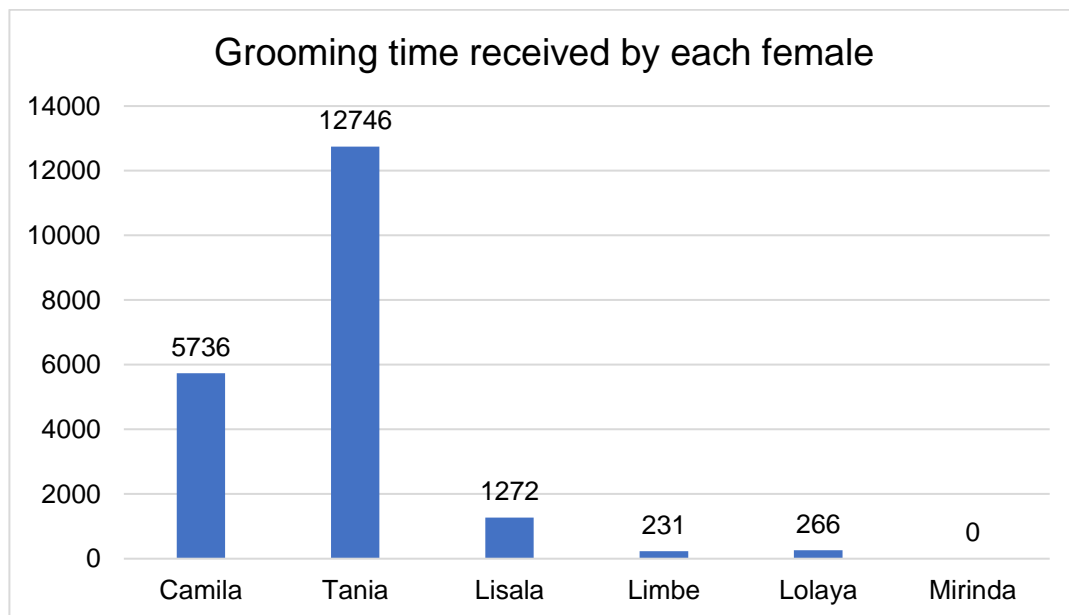
Figure 11: Received grooming time (in seconds) by each female.

Grooming time directed up the hierarchy

Camila	Tânia	Lisala	Limbe	Lolaya	Mirinda
0	800	4606	1294	3632	0
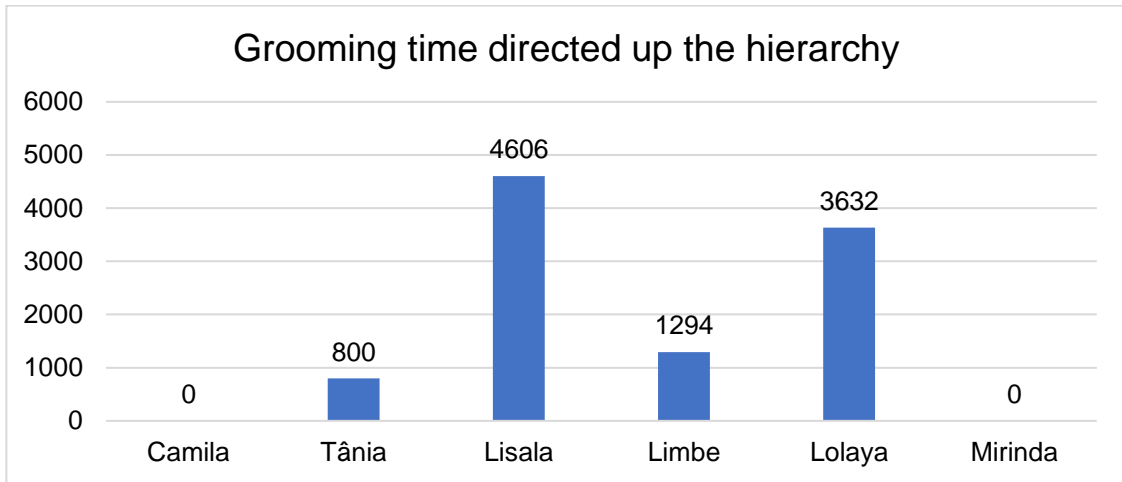
Figure 12: Grooming time (in seconds) that each female directed up the hierarchy.

Table 4: Proximity time between females (seconds).

Proximity (seconds)	Camila	Tânia	Lisala	Limbe	Lolaya	Mirinda
Camila						
Tânia	6883					
Lisala	6766	8428				
Limbe	3465	6244	5143			
Lolaya	1549	4986	1460	842		
Mirinda	99	233	27	193	0	

Table 5: Time in AR between females (seconds).

AR (seconds)	Camila	Tânia	Lisala	Limbe	Lolaya	Mirinda
Camila						
Tânia	4875					
Lisala	2528	912				
Limbe	417	265	168			
Lolaya	100	1962	28	0		
Mirinda	0	0	0	0	0	

Table 6: Time in ARE between females (seconds).

ARE (seconds)	Camila	Tânia	Lisala	Limbe	Lolaya	Mirinda
Camila						
Tânia	1737					
Lisala	650	1365				
Limbe	725	126	263			
Lolaya	0	81	27	0		
Mirinda	0	0	0	0	0	

Table 7: Grooming partnerships of each focal individual (the percentage of grooming that was direct towards each female by the groomer is indicated in parentheses).

Females (groomer)	Grooming partnerships (groomed)		
Camila	Tânia (87%)	Lisala (10.6%)	Limbe (2.3%)
Tânia	Camila (75.8%)	Lisala (0.4%)	Lolaya (23.8%)
Lisala	Camila (83%)	Tânia (16.7%)	Lolaya (0.3%)
Limbe	Camila (82.7%)	Lisala (17.3%)	
Lolaya	Camila (0.9%)	Tânia (98.6%)	Lisala (0.5%)
Mirinda			

3.2 Dominance and rank

The dominance hierarchy was calculated through 282 supplants and avoidances. The DI score for each female is presented in Table 8. Since Mirinda did not trade any grooming, I assumed that Mirinda was below Lolaya's rank.

Table 8: DI scores and relative ranking (RR) scores for each female.

Female	DI score	RR score
Camila	1.00	1
Tânia	0.99	2
Lisala	0.60	3
Limbe	0.41	4
Lolaya	0	5
Mirinda	0	6

Based on Pereira *et al.* (2019) data, the hierarchy steepness for 2016 and 2018 was calculated as 0.904 and 0.905, respectively. In 2020 the steepness decreased to approximately 0.60 (Figure 13). The overall patterns observed after calculating David's scores were similar to the DI results in 2016 and 2018. Two exceptions were observed in 2020 where Mirinda was placed above Lolaya and Tânia was placed above Camila (Tables 8 and 9), although the DI did not indicate a switch in ranks between the two females (Table A15 shows the DI scores for all periods; Table 9 and Figure 13 shows the David's score values).

Table 9: David's scores (DS) and normalized David's scores (normDS) for each female, for each independent period. The ND (No data) values were attributed to absent or non-sampled females.

Female's name	2016		2018		2020	
	DS	normDS	DS	normDS	DS	normDS
Camila	12.94	4.66	18.47	5.64	6.34	3.56
Tânia	ND	ND	13.84	4.98	8.54	3.92
Lisala	8.97	3.99	6.72	3.96	2.71	2.95
Limbe	3.04	3.01	0.10	3.01	-1.84	2.19
Lolaya	-3.46	1.92	-13.52	1.07	-8.99	1.00
Mirinda	-7.84	1.19	-8.05	1.85	-6.77	1.37
Nefertari	-13.65	0.23	-17.55	0.49	ND	ND
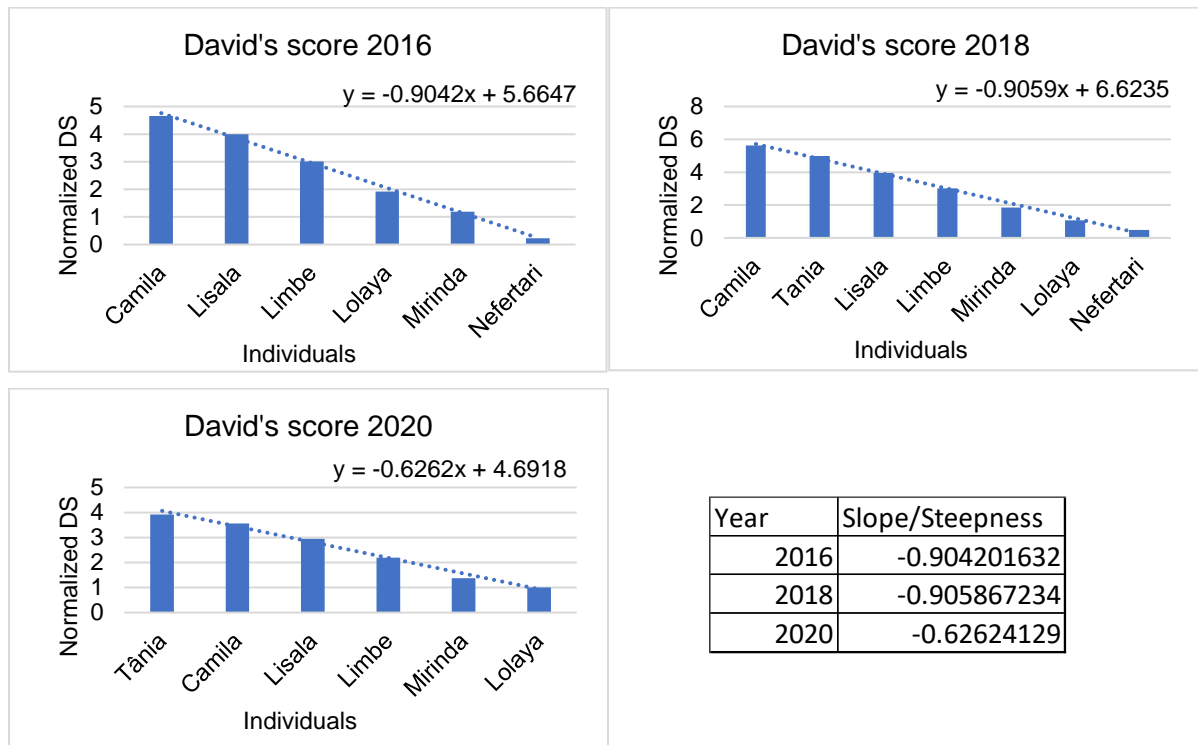
Figure 13: David's score for 2016, 2018 and 2020, with the slope indicating the hierarchy steepness for each independent period.

3.3 Effects of social rank on grooming

Confirming our first hypothesis (H_1), the Spearman's rank correlation results showed that higher-ranking females received more grooming than low-ranking females [(R = 0.928, N=6, P = 0.008), see Table 10 for a summary of the results]. When looking at grooming directed up the hierarchy (H_2), more than half (51.20%) was directed up the hierarchy. The Wilcoxon signed-rank test showed a significant difference between the observed and expected grooming directed up the hierarchy, supporting H_2 [(P = 0.068, N = 4), Table 10]. The observed values of grooming directed up the hierarchy were higher than expected, with the calculated value of expected grooming directed up the hierarchy being smaller than the observed value of grooming directed up the hierarchy.

I found no support to the hypothesis that grooming was more reciprocally traded between individuals closer in rank (H_3), as the tau K_r showed no significant relationship between the hierarchy distance matrix and the reciprocity index matrix [(tau K_r = 0.225, P = 0.347, N = 5), Table 10].

3.4 Grooming reciprocity. Grooming as a "resource" traded not only for other commodities but also for itself.

Using the tau K_r test, I conducted a correlation test between the matrices of grooming given and received and obtained a positive and significant correlation (tau K_r = 0.512, P = 0.017, N = 5) providing support to our H_4 that females reciprocally trade grooming with each other (Table 10).

3.5 Partner choice for grooming

Females groomed up to three other females, and diversity index values of grooming partners were low [(H'): mean = 0.275]). When computing the correlation between both binary matrices of partnerships from 2018 and 2020, the tau K_r test showed that, as previously hypothesised (H_5), females maintained their partner choices from 2018 to 2020 [(tau K_r = 0.867, N = 6, P = 0.003), Table 10].

3.6 Tolerance

I found no support for the hypothesis (H_6) that grooming is traded for social tolerance (decrease in agonistic behaviour). I did not observe a significant negative correlation between high values of grooming with low values of aggressive interactions between dyads (tau K_r = -0.361, N= 6, P = 0.067). Nevertheless, a significant correlation between grooming traded and ARE was observed (tau K_r = 0.667, N=6, P = 0.009), highlighting the possibility that grooming is traded for social tolerance in the form of access to food (Table 10).

Table 10: Summary of the main results.

Hypothesis		Results
H_1	High-ranking females receive more grooming than low-ranking females	Yes
H_2	Grooming is directed up the hierarchy	Yes
H_3	Grooming is more reciprocally traded between individuals closer in rank	No
H_4	Grooming reciprocity	Yes
H_5	Partner choice maintained	Yes
H_5	Grooming diversity index values	Low
$H_{6 - \text{First test}}$	Grooming is traded for social tolerance (decrease in agonistic behaviour)	No
$H_{6 - \text{Second test}}$	Grooming is traded for social tolerance (Increase in ARE)	Yes

4. Discussion

As aforementioned, this thesis aimed to address not only the data that was collected in 2020 but also to compare it with previous information from the same mandrill colony, collected in 2016 and 2018 by Pereira *et al.* (2019) which is presented in the Annex A. I intended to analyse the results collected over these three consecutive data collection periods in order to better understand the social behaviour dynamics (namely grooming) among mandrills.

The hypotheses in this work closely follow those presented by Pereira *et al.* (2019). However, this thesis allows for a more in-depth analysis of ranking effects on commodities exchange between colony members, especially on a long-term basis. Besides, since female mandrills have a considerably long life expectancy (Setchell *et al.*, 2005a), and relationships in primates can endure for a life-time (Hammerstein and Noe, 2016), this dissertation offers more than a snapshot of female mandrill social behaviour by analysing long term data on grooming dynamics.

As the colony suffered sensible changes since 2018 (e.g., the death of the female Nefertari and, more recently, competition between the males Mapendo and Kunta for the dominance of the group), one could envision that these alterations may have affected the group social dynamics, leading to changes in the preferred grooming partners. To test this and other hypotheses, I mainly resorted to the use of grooming data from focal samplings. As a cautionary note, I should point out that, even though allogrooming is one of the most important social behaviours in primates, often used as a proxy for the study of social relationships (Dunbar, 2010), one must keep in mind that a single behaviour might not always represent the full extent of social relationships (Smith-Aguilar *et al.*, 2019).

Before discussing the previously raised hypotheses, it is important to understand the hierarchical characteristics that the colony possessed. With David's scores values calculated for the 2016, 2018 and 2020 periods (Table 9 and Figure 13), together with the DI scores (Table A15) I can analyse the characteristics of dominance and submissive relationships between group individuals. Since an increase in hierarchy steepness leads to an increase in grooming traded for agonistic support (Balasubramaniam *et al.*, 2012) and since agonistic support is a rank related commodity (Newton-Fisher and Kaburu, 2017), an increase in steepness should also lead to an increase of grooming time directed up the hierarchy. On the other hand, a decrease in steepness should redirect grooming to be more reciprocally traded (Barrett *et al.*, 2002; Barrett *et al.*, 1999).

From Table A15, one can see that the dominance rank of the Badoca Safari Park colony, which includes three distinct periods of time [2016, 2018 from Pereira *et al.* (2019) and 2020), suffered minor changes across these three periods. Some of the more noticeable changes occurred with Lolaya's rank which went from fourth place in 2016 to sixth in 2018 and ended in fifth place in 2020. In 2018, Tânia established herself in second place on the hierarchy, below Camila, reaching a DI score of 0.995 in 2020. It is important to mention that the reason why Tânia's DI score is 0.995 instead of 1, is due to a single supplant episode, delivered by Limbe. From David's score results I can globally observe the same pattern of ranking scores in all periods with the exception of 2020, where Camila is placed below Tânia and Lolaya is placed below Mirinda. Such results may not represent a sensible decrease of dominance from Camila or Lolaya, as they may simply be due to the high number of supplants delivered by Tânia and received by Lolaya in 2020 (which David's score is more sensible to). By analysing the grooming that each female directed up the hierarchy (Figure A16) and the hierarchy steepness values for each period (Figure 13 and Table 9), the total amount of grooming given by each female should be superior in 2016 and 2018 since the steepness values in 2016 and 2018 were higher than in 2020 (Balasubramaniam *et al.*, 2012; Newton-Fisher and Kaburu, 2017). Yet, the grooming time directed up the hierarchy by each female does not seem to have been influenced by the steepness of the hierarchy, with Lolaya even increasing her given grooming up the hierarchy in 2020. If we analyse the grooming time directed up the hierarchy by Limbe and Lisala [middle-rank females, which are supposed to more easily exchange grooming up and down the hierarchy (Xia *et al.*, 2021)], such effect of the steepness remains imperceptible and the same applies to Tânia.

The steepness of the hierarchy could also be reflected by a simple increase of grooming time not exclusively directed up the hierarchy (Barrett *et al.*, 1999; Dunbar, 2010) which was also not perceptible (Figure A14). Results show that despite steepness remained high in all periods, some changes occurred on the ranks and partnerships quality, which is reflected on the grooming that each female traded with each other. For example, a substantial amount of the grooming traded in 2016 by the three lower-ranking females was conducted between Mirinda and Nefertari (Table A11). Nefertari, in 2016, may have received superior amounts of grooming than she would normally receive due to a possible "baby market" effect (Henzi and Barrett, 2002) and not as a response to the increased risk of aggressiveness associated with the high value of hierarchy steepness. The "baby market" effect is a hypothesis that defends that babies are seen as a tradable "resource" in which mothers receive grooming in exchange for access to the infant (Henzi and Barrett, 2002). Supporting this observation is the fact that, in 2016, Nefertari received more than 6000 seconds of grooming and, in 2018, received no grooming (Table A12). It seems that from 2016 to 2018,

with the independence of the infant, the value of Nefertari as a grooming partner changed, since the infant, in a marketplace, consists of a "volatile" commodity whose value can rapidly change as the infant matures (Dunayer and Berman, 2016). Such change could have triggered adjustments in partnerships. In 2016, Lolaya directed 87.5% of her grooming to Mirinda, and suddenly, in 2018 no grooming was traded between both females. A similar observation can be made between Mirinda and Nefertari, with Mirinda directing 80.8% (Table A13) of her grooming to Nefertari (5832 seconds of grooming) with a sudden suspension of grooming trade between both females in 2018 (Tables A11-A12). Such changes surely influenced their values as possible allies leading to a decrease of interest in maintaining grooming partnerships with both Mirinda and Nefertari.

Since grooming is time-limited (Noe and Hammerstein, 1995; Schino, 2001; Seyfarth, 1977), Nefertari and Mirinda suffered a deep decrease on the grooming received by other females, and Lolaya, on the other hand, seems to have redirected her attention into the establishment and/or fortification of a partnership with Tânia, a higher-ranking female to whom she directed 80.1% of her grooming in 2018 (Table A14), leading to an increase of Lolaya's grooming directed up the hierarchy. From 2018 to 2020, Lolaya maintained her partnership with Tânia and, despite the decrease of steepness that should lower the need of low-ranking females to direct grooming up the hierarchy, the grooming given by Lolaya to Tânia increased to 98.6% (Table 7), confirming that Lolaya displayed a clear preference towards Tânia, instead of Mirinda which was her main grooming target in 2016. From 2018 to 2020, with the death of Nefertari, Mirinda became socially excluded from the group. Changes in rank and grooming distribution can be possibly explained by the maturation of Tânia [proposed by Pereira *et al.* (2019)], the exclusion of Nefertari and Mirinda from the "grooming market" (in 2018 and 2020, respectively) and the death of Nefertari.

In conclusion for the steepness analysis, the increase in steepness should lead to a more distant hierarchy status between females, both at the top-down and bottom-up levels, increasing the demand for grooming as a social tool since the biological market theory integrates competitive regimes, dominance gradients and grooming relationships (Barrett *et al.*, 1999). Yet, results do not seem to support the presence of such an effect in the studied colony. It is possible that the low number of females in the colony, together with the fact that some females were socially excluded from the group, limited my ability to detect such effects. With a basic understanding of the hierarchy changes and the effects that such changes may have caused on the colony, from 2016 to 2020, I can better analyse this dissertation tests results for each hypothesis.

Results presented in this dissertation regarding the effects of rank on grooming are complex. The tests for H_1, H_2 and H_3 were set out to help us further understand the effects of

rank on the distribution of grooming within colony members. Results from the tests for H_1 and H_2 display evidence that rank had a strong effect on the grooming distribution amongst colony members. In summary, when testing if higher-ranking females receive more grooming than lower-ranking females (H_1) and if females direct their grooming up the hierarchy (H_2), my results show that grooming was both directed up the hierarchy and females received more grooming according to their rank. Since individuals did not groom others of similar rank more often (H_3) this means that the effects of rank were strong in the grooming patterns and that distance in the hierarchy played a small role in the establishment of grooming partnerships (Kaburu and Newton-Fisher, 2015; Pereira *et al.*, 2019; Schino, 2001; Schino and Lasio, 2018; Seyfarth, 1977).

The confirmation of H_1 and H_2 means that higher-ranking females were more valuable than lower-ranking females likely due to their capacity of delivering ranking-related commodities. From H_1-H_2 tests results, it became clear that higher-ranking females are valuable partners in the trade of grooming. This corroborates the results established and debated on the meta-analyses (Kaburu and Newton-Fisher, 2015; Pereira *et al.*, 2019; Schino, 2001; Schino and Lasio, 2018; Seyfarth, 1977) in which high-ranking females were either able to monopolize grooming, or lower-ranking females directed grooming up the hierarchy in an attempt to receive rank related commodities or establish high valuable partnerships, also giving support to the Seyfarth (1977) model. Pereira *et al.* (2019) suggested that the inclusion of Tânia as a mature female in 2018 created instability among the structure of the hierarchy by increasing the effect of rank on the trade of grooming, creating a more unbalanced dominance relationship amongst females. The increase of dominance discrepancy between females should lead to an increase of the value of grooming given by high-ranking females, creating a market where grooming from high ranking-females is more valuable than grooming provided by low-ranking females (Barrett *et al.*, 1999). Such increase of dominance discrepancy should be reflected in an increase of the hierarchy steepness values (de Vries *et al.*, 2006). Yet, in 2018 the year that Tânia was introduced to the focal sampling, the steepness remained similar to 2016.

Despite the steepness not showing alterations with the inclusion of Tânia, the hierarchy was very steep in both periods (2016 and 2018). Yet, in 2018 the number of mature females increased from 6 to 7 which, as previously argued, has the potential to provoke changes in the grooming patterns (Barrett and Henzi, 2002; Casanova, 2002; de Waal, 2000; Noe and Hammerstein, 1995). This can be so for at least two reasons: first, it brings a new individual to the grooming competition; second, Tânia occupied the second rank in the hierarchy. Being a high-ranking female, her value as a grooming partner was likely superior to any other individual below her rank. With this additional high-ranking female (Tânia), some grooming

may have been redirected from lower-ranking females towards Tânia, and in fact one can see an increase in grooming directed up the hierarchy with 25.76% in 2016 and 78.93% in 2018. Since high-ranking females have less necessity to reciprocate and are more desirable as grooming partners, the addiction of Tânia, may have increased the grooming time directed up the hierarchy, even though the steepness remained similar in both periods. In 2020, despite the fact that the hierarchy became shallower, some degree of steepness persisted. Such decrease could be the result of a decrease in partnership competition with the decrease in population density together with the exclusion of Mirinda from the social group.

The hierarchy steepness values showed that, across the three periods of data collection, dominance relationships were very steep with discrepancy in dominance in all periods (despite the decrease in steepness in 2020). In such hierarchical scenario, grooming given by higher-ranking females is more valuable than grooming given by lower-ranking females (Barrett *et al.*, 1999), leading to unbalanced relationships where high-ranking individuals receive more grooming. The test results for accessing if grooming is more reciprocally traded between individuals closer in rank (H_3) also suggest that the ranking of the receiver was more important than the ranking of the giver to explain grooming distribution and that the existing discrepancy on the hierarchy lead to a decreased necessity or desire to direct grooming towards females closer in rank. Summarizing, H1-H3 test results, which were similar to 2016 and 2018 Pereira *et al.* (2019) results (Table A16), show that in hierarchies characterized by unbalanced dominance relationships (steeper hierarchies), females direct their efforts into establishing grooming partnerships with higher-ranking females (H_1 and H_2, topic 3.3) instead of choosing individuals of similar status (H_3, topic 3.3), which may not be able to deliver rank-related commodities as effectively as higher-raking females (Barrett *et al.*, 1999; Seyfarth, 1977). Although H_3 was not confirmed, H_1-H_2 tests results shed light to some of the predictions established by the Seyfarth (1977) model (topic 1.6). Otherwise, if high-ranking females could not deliver rank-related commodities or if low-ranking females did not require them, the predictions in H_1 and H_2 would not be fulfilled.

The tests elaborated to access if grooming was reciprocally traded (H_4) and if partner choice was maintained (H_5) allowed us to understand the importance of grooming as a commodity (Henzi and Barrett, 1999) and the longevity of partner choices maintained over long periods of time. Data from 2020 allowed me to analyse an extended period for grooming trade and partner-choice maintenance. I was able to confirm that grooming was reciprocally traded in 2020, and the maintenance of partner-choice over a period of four years despite some changes in the colony, such as the maturation of Tânia, maturation of the male Bantu (which was dependent on Nefertari in 2016), Mogli's birth (Lolaia's son) between 2016 and 2018, and the death of Nefertari between 2018 and 2020. When analysing partnerships, one

can look to the time each individual spends trading grooming and in proximity allowing for a better perspective of the relationship quality. For example, when looking to the grooming trade and time spent in proximity (Tables 3, 4, 5 and 6) between individuals in 2020, there are two females that, despite occupying distant rank positions, showed signs of an established strong relationship. Data from 2018 and 2020 showed that Lolaia and Tânia, in 2018 and 2020, traded a large amount of grooming and it was reported by Pereira (personal observation) that, in 2016, both females already had formed a partnership, which was not registered because Tânia was still immature. Since these females occupy distant ranks, it seems likely that they developed a strong relationship. The confirmation of partner-choice maintenance (H5) and reciprocity (H4) among group females, together with the example of Lolaya and Tânia, gives support to the idea that an emotional bookkeeping mechanism (Aureli and Schaffner, 2002; Schino and Aureli, 2010), based on the accumulation of emotional experiences [such as grooming trade (Hammerstein and Noe, 2016)], can contribute to the maintenance and regulation of grooming partnerships between colony members.

My results, together with the results reported by Pereira *et al.* (2019) which confirmed the absence of immediate reciprocity, support the notion that grooming traded over time has a strong impact on the stability of grooming partnerships (Schino and Pellegrini, 2009). Likewise, after a long and continuous period of collected data, Schino and Pellegrini (2009) found that immediately traded grooming may not play an important role in long-term partnerships in captive mandrills. The results obtained by Schino and Pellegrini (2009) and Pereira *et al.* (2019) suggested that long-term traded grooming is the main factor regulating long-term partnerships and, as one can see by the 2020 results, partner-choice was maintained and grooming continued to be reciprocally traded between individuals in the long term. This suggests that grooming traded over time builds up positive feelings that should fortify and stabilize grooming partnerships.

From the results of the reciprocity test (H4) I can assume that even though grooming can be traded by other commodities, it remained a valuable commodity to be traded by itself. Regarding the maintenance of partner-choice (H_5), results showed that females had a clear partner preference not only for each period but also across periods (Tables 7, A13 and A14). With the data from 2020, one can see that preferences remained similar across long periods of time. The observed stability of partner choice supports the hypothesis that choosing only some specific individuals is a common strategy by Cercopithecoidea species (Crockford *et al.*, 2008; Engh *et al.*, 2006; Silk *et al.*, 2012). For example, the clear preference of Lolaya for Tânia as a grooming partner shows a clear effort from Lolaya to maintain and fortify the partnership with Tânia, directing most of her grooming effort to her (Goosen, 1981; Kummer, 1978) which may be a partnership with potential trade for high-ranking related commodities.

One must keep in mind that group-living species are subject to a dynamic social life and changes in social interactions and partnerships are expected to occur over time as a result of stochastic factors as well as changes in factors such as group composition, social hierarchy, and other intrinsic properties of group life (Barrett and Henzi, 2002; Casanova, 2002; de Waal, 2000; Noe and Hammerstein, 1995). The results from Pereira *et al.* (2019), together with the results reported in this thesis, suggest that the stability of the captivity environment and the absence of major demographic shifts between the three observational periods created a stable environment that allowed females to maintain their previously established grooming partnerships (Dunayer and Berman, 2016; Hammerstein and Noe, 2016). Demographic changes, such as the independence of an infant (Banto), the birth of a new group member (Mogli) and maturation of a female (Tânia), are considered small scale changes that are common in primates societies. Since social partnerships have the potential to endure a lifetime (Hammerstein and Noe, 2016), it is not expected for normal demographic changes to result in deep changes of the established grooming partnerships within a group. The stability of such partnerships could turn out to be beneficial since individuals would not need to direct effort into the establishment of new partnerships.

To understand if grooming was being traded by social tolerance (H_6), in 2020, I conducted two tests to access H_6. If grooming was indeed being traded by social tolerance, one could expect a decrease in aggressive behaviours from the groomed individual. For 2016 and 2018, the results reported by Pereira *et al.* (2019) confirmed the prediction from the trade model that higher power differentials potentiate the trade of grooming for rank-related commodities (Barrett *et al.*, 1999). This was evident through a significant negative correlation between grooming and agonistic interactions. However, for the 2020 period, the test to assess H_6 did not support that grooming was traded for a decrease in aggressiveness towards the groomer. The steepness value of the hierarchy showed that the hierarchy was shallower in 2020 and that the dominance pressure within females was diminished. The decrease in the hierarchy steepness likely resulted in a decrease in the trade of grooming for rank-related commodities, such as agonistic support or aggressiveness decrease (Balasubramaniam *et al.*, 2012; Newton-Fisher and Kaburu, 2017). It is also important to notice that the analysis employed to test this hypothesis here and in Pereira et al. (2019) are correlational. Because grooming facilitates bonding (Dunbar (2010), the findings reported are subject to the possibility of reflecting existing friendships rather than the trade between grooming and tolerance in a marketplace (Dunbar, 2010; Pereira *et al.*, 2019).

Despite not obtaining confirmation of the trade of grooming for aggressiveness decrease, social tolerance may not be only delivered through a decrease in aggressiveness. Recently, a study from Tiddi *et al.* (2012) showed that, even though grooming appeared to be

traded by rank related benefits, higher-ranking females did not seem to deliver agonistic support or even decrease aggression in return for grooming. Tiddi *et al.* (2011) argued that females competed with each other for access to certain preferential locations (in their case, the central position in the spatial proximity network of the males) that were controlled by dominant individuals. In our study, it is possible that females are trading grooming for the opportunity to occupy certain island locations or for tolerance while searching for food or eating which are rank related commodities (Tiddi *et al.*, 2012; Tiddi *et al.*, 2011). This way, females (especially high-ranking females) continued to practice agonistic behaviours towards more submissive females and instead of decreasing aggressiveness in exchange of grooming, they would allow submissive females access to food. In the studied colony, one can easily verify that food is abundant rendering competition for food as an unlikely scenario. Nevertheless, it must be acknowledged that, in some captive groups, high-ranking individuals still try to monopolise access to food (de Waal, 2007).

Since the results from H_1-H_3 confirmed that higher-ranking females benefit from the grooming trade, one possible alternative to aggressiveness decrease could be access to preferred types of food. In such a scenario, it is possible that higher-ranking females limited the access of lower-ranking females to a specific food. In this situation, low-ranking females might attempt to gain "permission" from higher-ranking females to access such food. In fact, the mandrill colony from Badoca Safari Park did show a preference for seeds and these were spread every morning in the peripheral edges of the island. The zone of the island covered by trees had fewer seeds available, resulting in most females searching for seeds every morning around the island, ignoring the centre. Lower-ranking females may thus direct their grooming up the hierarchy to receive social tolerance from higher-ranking females while searching for food (Tiddi *et al.*, 2012). For example, Mirinda did not trade any grooming, and was never observed searching for food alongside any other female which is reflected in the amount of time she spent in ARE with other females. This hypothesis, of grooming being traded for access to a specific type of food, instead of a decrease in aggressiveness, is supported by the additional test conducted for H_6, in which increased ARE time was correlated with an increase in grooming traded, showing that grooming could have been traded and directed up the hierarchy for the exchange of social tolerance while searching for a specific type of food [tolerance to access food; see Seyfarth and Cheney (1984)]. In summary, the results for H_6 did not entirely support the hypothesis that grooming was traded for a decrease in aggressiveness toward the groomer (social tolerance). Once again, considering the steepness of the hierarchy, the decrease in steepness should be accompanied by a decrease in grooming being traded for some rank-related commodities such as agonistic support and aggressiveness decrease (Balasubramaniam *et al.*, 2012; Newton-Fisher and Kaburu, 2017).

This would lead to changes in market values resulting in alterations of the grooming distribution (Table 7, A13 and A14), matching the results of the correlation test of grooming and agonistic interactions conducted in H_6, with individuals no longer exchanging grooming for decreased aggressiveness. Results from the correlation between grooming and ARE time, used to assess if grooming was traded for access to food, show that there was a replacement of traded commodities, with high-ranking females exchanging social tolerance for grooming. Instead of a decrease in aggressiveness, tolerance while eating or searching for food could have been the main type of social tolerance being trade in 2020 (Seyfarth and Cheney, 1984).

In the studied colony, another element that could have impacted social behaviour and the trade market itself was the type, availability and position of the resting spots or simply the spatial position within the group. Group-living animals tend to favour the occupation of some specific locations. Following what was proposed by Hamilton (1971), group-living individuals exhibit preferential positions in the space occupied by the group, typically preferentially gravitating towards the centre of the group. For example, individuals located at the edge of a territory/community area are expected to experience a higher risk of predation, converting the centre into the most desired location to occupy (Hamilton, 1971). This "marginal effect" is well-supported by empirical evidence on different taxa (Krause, 1994; Stankowich, 2003). Even though there is no predation risk on the island, it was evident during the observations that the two higher-ranking females, Camila and Tânia (sometimes even Lisala), spent most of their time in the centre of the island (personal observation), whereas the others occupied more peripheral areas. The best example was Mirinda who spent most of the time distant from the group, on the edge of the island, avoiding social contact as much as possible. It is possible that, besides access to food, spatial positioning in a captive enclosure also constitutes a commodity with considerable value. If so, higher-ranking females could trade this commodity (e.g., allowing other females to remain, rest, eat or scavenge for food during specific periods of the day) for other resources (e.g., grooming).

Despite the absence of predators, the centre of the island continues to offer protection with the natural and man-made structures from noise and weather, also allowing for an added level of privacy from the park visitors. It seems likely that there are preferential positions in the island derived at least from protection from weather conditions and centrality within the group. Such conditions may have influenced the social behaviour of the group. Regarding the captivity conditions, it seems unlikely that the captivity environment promoted agonistic behaviours between females. Yet, as discussed, the specific location within the outdoor installation (Figure 6) could be the target of competition between individuals leading, for instance, to the exchange of grooming, not for an agonistic decrease toward the groomer, but actually for the exchange of grooming for spatial tolerance in specific spots in the island.

Summarizing the results for all three periods available, one must keep in mind that some individuals were either not present in all periods (Nefertari) or were not mature in all observations periods (Tânia). This way, grooming data was not collected from Tânia in 2016 (she was not a mature female), and between 2018 and 2020, Nefertari died. These changes were expected to influence the patterning of social interactions within the group and, therefore, the patterns and dynamics of the grooming interactions (de Waal, 2000; Noe and Hammerstein, 1995). Comparing the results from all three time periods (Table A16 displays the dynamics of the different social parameters that were tested on the mandrill colony in 2016, 2018 and 2020), I detected that, with the exception of 2016, the tendency for high-raking females to receive more grooming than low-ranking females was confirmed (H_1; Topic 3.4). Grooming given was directed up the hierarchy in all periods of data collection (H_2, topic 3.4) showing that high-ranking females were more valuable as grooming partners. Grooming was never confirmed to be more reciprocally traded between individuals closer in rank (H_3, topic 3.3). Reciprocity in grooming was also confirmed in all periods (H_4, topic 3.4). Partner choice was maintained both from 2016 to 2018 and from 2018 to 2020 (H_5, topic 3.5) and grooming diversity index values were low in all periods[3] (H_5, topic 3.5) corroborating the hypothesis that mandrills follow the common strategy of other Cercopithecoidea species in which they chose a limited number of partnerships just as already discussed (Crockford *et al.*, 2008; Engh *et al.*, 2006; Silk *et al.*, 2012). Grooming was confirmed to be traded for social tolerance (in the form of decreased agonistic behaviours towards the groomer) in 2016 and 2018 but not in 2020 (H_6, topic 3.6). Yet, in 2020, grooming seemed to have been traded for a different type of social tolerance in the form of access to food [the increased grooming traded seemed to increase the tolerance of the groomed while at ARE; (H_6, topic 3.6)].

Finally, it is important to point out the importance of behavioural studies for colony monitoring. Such studies can help us understand the current relationships between individuals and may help to identify "vulnerable" colony members. For example, the conditions leading to the social exclusion, in 2018, of one colony member (Nefertati) strongly suggests that a similar event might occur in the near future (Mirinda). In 2018, Pereira *et al.* (2019) reported that Nefertari was excluded from the grooming network and that she was aggressively pursued by the alpha male and by the highest-ranking female. Ten days after the end of data collection, in 2018, Nefertari died. Presently, it is possible to observe a similar scenario involving Mirinda, who has been similarly excluded from the grooming network. She was also subjected to supplants and pursues from all the other females (except Lolaya). The alpha male did not

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[3] Computations with the 2016 and 2018 data [by Pereira et al. (2019)] showed that the six to seven females included in the test groomed only between one and three other females of the colony, and that grooming diversity index values were generally low (2016 (H'): mean = 0.299; 2018 (H'): mean= 0.317).

actively pursue Mirinda who spent most of her time excluded from the proximity of any colony member, an observation clearly reflected in the time spent in proximity, AR and ARE (Tables 4, 5 and 6). This suggests that, like Nefertari, Mirinda may soon become the target of aggressive harassment conducted not only by the dominant male but also by the dominant females. Following the observations from Pereira *et al.* (2019) on Nefertari, in 2018, I hypothesise that Mirinda may also suffer the adverse consequences of exclusion from the group since she is now the omega female. In the wild, the social exclusion would likely impact the individual's fitness associated with an increased rate of mortality [and the eventual migration of the ostracised individual (Lancaster, 1986)]. In a captivity enclosure environment, an excluded female is unable to migrate. As such, cases of social exclusion need to be identified and monitored to safeguard the well-being of all individuals, especially that of the rejected individual. Alternatively, the reduced sociality of Mirinda could be the result of her advanced age. If this is indeed the case, the observation of older social pariahs, such as Mirinda or Nefertari, could provide valuable insights into how mandrill societies cope with ageing.

5. Conclusion

In this study, the grooming interactions of a colony of mandrills were studied. I also compared results with those from previous studies, on the same colony, in 2016 and 2018. In this study, I characterised three main features of grooming interactions in a marketplace (BMT): grooming patterns, grooming trade and grooming partner choice.

Results helped to better understand how grooming interactions are regulated within a true matrilineal colony of mandrills. The results reinforce the idea that female mandrills follow common Cercopithecoidea social strategies, namely by maintaining partner choices and engaging with only a few partners in stable demographic conditions (Crockford *et al.*, 2008; Engh *et al.*, 2006; Silk *et al.*, 2012). Under these conditions, grooming interactions remain stable and can be explained by the BMT, with grooming possibly being traded by other commodities, such as social tolerance.

With the analysis of David's score values, I was able to calculate the hierarchy steepness and elaborate a deeper analysis upon the results of the tests for each hypothesis. When comparing my results with those from 2016 and 2018, I was able to conclude that, when hierarchy steepness values decreased, a shift on the traded commodities occurred, and grooming trade for agonistic support decreased. High-ranking females adapted to the new market conditions by trading other types of social tolerance.

The results from this study also show that it is important to regularly track the social relationships in a primate colony since monitoring can help improve the management of the captive animals by providing early warning signs of potential social exclusions. This would give keepers time to assess possible threats and prevent serious attacks on ostracized individuals (or even to prevent deaths).

One limitation of our study was the sample size. My work was conducted with six females and prior studies worked with a similar group size of either six or seven females. It is abundantly known that small sample sizes limit the array of potentially usable statistical tests, while also decreasing their power. Still, one must consider that i) mandrill colonies in captivity are scarce (especially one with a true matrilineal line) and understandably contain fewer individuals than natural mandrill groups, and ii) data on the social dynamics of mandrills is still virtually absent. Thus, despite potential limitations, I feel that the presented results are potentially useful for both researchers, wildlife managers and zookeepers. Mandrills are an under-studied primate species and remain one of the most difficult primate species to study in the wild (Setchell, 2016). Also, studies on a true matrilineal colony are equally infrequent. This colony consists of a true matrilineal group and, contrary to those studied in other works (e.g.

Schino and Lasio (2018), more closely mirrors the natural social interactions observed in the wild (Abernethy *et al.*, 2002). The necessity to understand the social dynamics of mandrill societies is urgent, especially in the current context of habitat destruction and bushmeat consumption. It is increasingly important to understand the ecology, behaviour and social organization of the species in a world where, during the last decades, so many species have disappeared or are facing extinction.

Given my results, I believe that future studies would benefit by looking into grooming distribution according to ranks via social network analysis in order to better understand other aspects of rank effects on the grooming dynamics. One element that could also help understand important elements of social dynamics would be to perform a territorial analysis for each female: by registering spatial locations during focal samplings, one could map and quantify the preferential locations of each individual, simultaneously allowing the analysis of territorial competition and a more rigorous testing of the possibility that grooming is being traded for access to preferential locations. Finally, the hypothesis related to access to food *vs* aggressiveness decrease should be addressed to see if whats types of social tolerance are traded for grooming and what factors drives individuals to trade such rank-related commodities.

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Images references

Figure 1. IUCN map of mandrill geographical distribution. URL: https://www.iucnredlist.org/es/species/12754/17952325#geographic-range

Figure 6. Island-like outdoor enclosure of the Badoca Safari Park mandrill colony (internal area = 1673.55 m2). URL: https://www.google.pt/maps (print)

Annex A

Results from 2016 and 2018

Through the directed grooming matrixes from 2016, 2018 (Tables A11-A12) collected by Pereira *et al.* (2019) I was able to analyse grooming distribution changes prior to my dissertation. In 2016, Mirinda was the female who gave more grooming and Lisala the female who gave less grooming (Figure A14). For 2018, Nefertari did not groom anyone. Lolaya was the female who gave most grooming and, by excluding Nefertari, Mirinda was the female who gave less grooming (Figure A14).

For the 2016 period, all females received grooming (Figure A15). The female receiving the most grooming was Nefertari. The female receiving less grooming was Lisala (Figure A15). In 2018 Mirinda and Nefertari did not receive any grooming. The female receiving most grooming was Tânia and the female receiving less was Lolaya (Figure A15).

In 2016 all females directed grooming up the hierarchy, with Mirinda giving most grooming and Lolaya giving less grooming (Figure A16). In 2018, Nefertari did not groom anyone up the hierarchy. Lolaya was the female who gave most grooming up the hierarchy and Mirinda, once again excluding Nefertari, was the female who gave less grooming up the hierarchy (Figure A16).

The grooming partnership results are presented in two tables for 2016 and 2018 (Tables A13-A14). Camila maintained a partnership over all periods with Lisala, Limbe and Tânia. Tânia maintained a partnership from 2018 to 2020 with Camila, Lisala and Lolaya. Limbe maintained a partnership with Camila and Lisala. Lolaya maintained a partnership with Tânia and Lisala. Mirinda and Nefertari did not maintain any partnership across the periods in which they were present.

Table A11: Directed grooming effort matrix for 2016 [from Pereira *et al.* (2019)]

Year 2016						
	Camila	Lisala	Limbe	Lolaya	Mirinda	Nefertari
Camila	0	312	894	0	0	0
Lisala	304	0	65	13	0	0
Limbe	850	108	0	0	0	0
Lolaya	0	164	0	0	2176	147
Mirinda	0	0	0	1389	0	5832
Nefertari	0	0	0	0	461	0

Table A12: Directed grooming effort matrix for 2018.

Year 2018							
	Camila	Tania	Lisala	Limbe	Mirinda	Lolaya	Nefertari
Camila	0	1293	243	79	0	0	0
Tania	265	0	36	0	0	121	0
Lisala	631	948	0	0	0	134	0
Limbe	1411	200	879	0	0	0	0
Mirinda	49	0	0	0	0	0	0
Lolaya	0	2334	579	0	0	0	0
Nefertari	0	0	0	0	0	0	0

Figure A14: Grooming time given by each female [2016, 2018 and 2020; a negative value (-1) was attributed to unsampled or absent females].
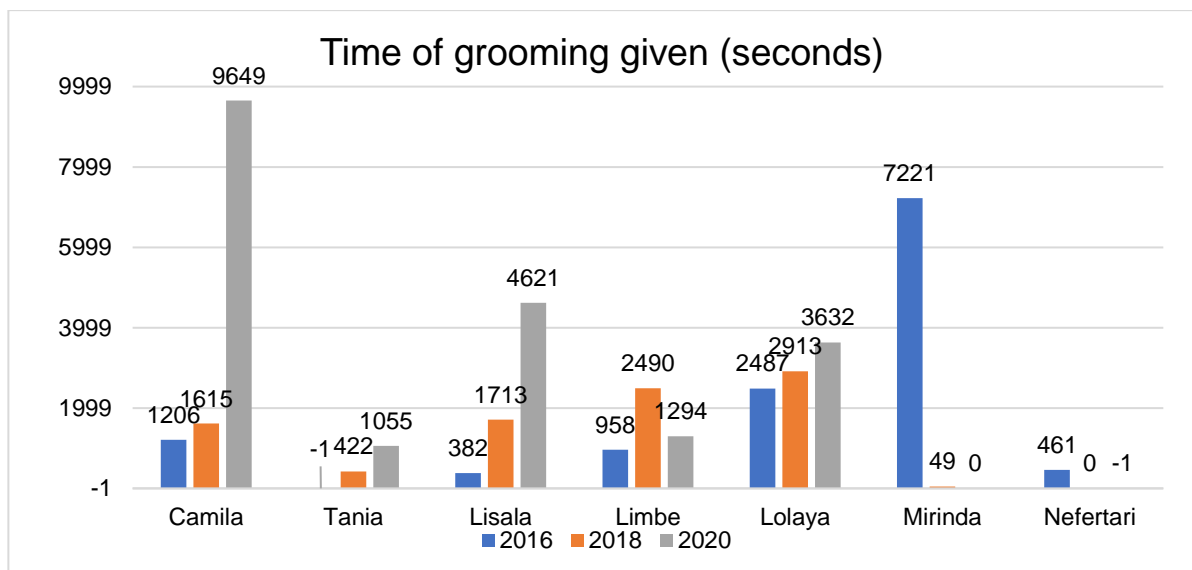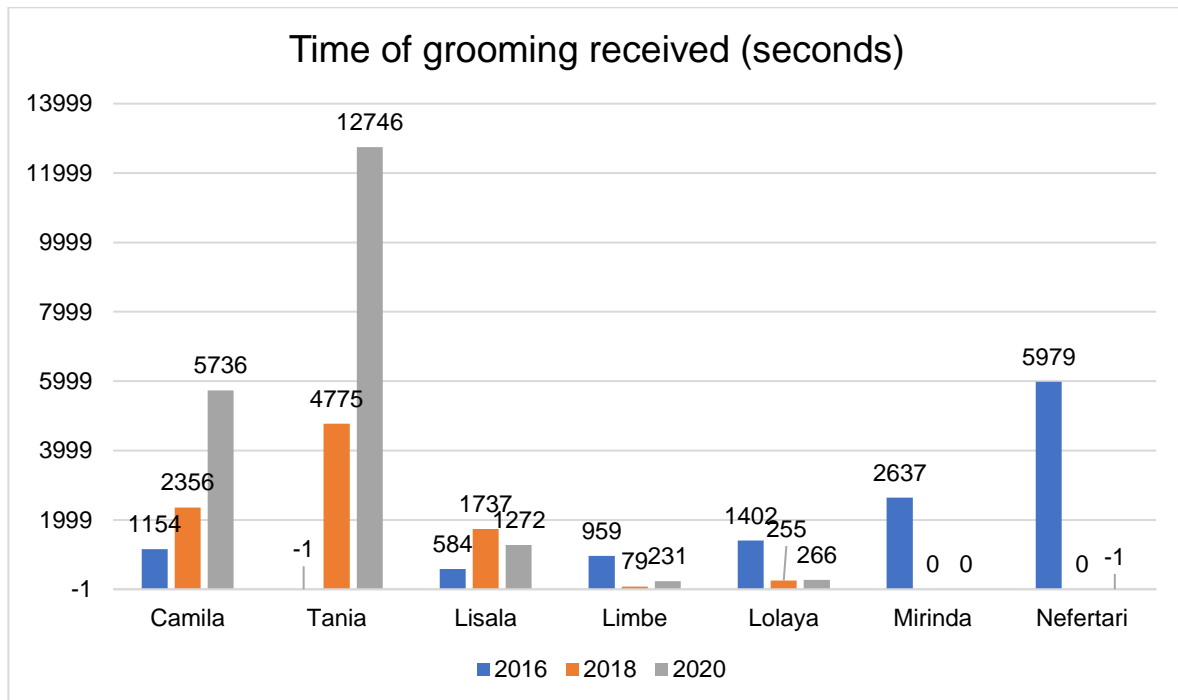
Figure A15: Grooming time received by each female [2016, 2018 and 2020; a negative value (-1) was attributed to unsampled or absent females].
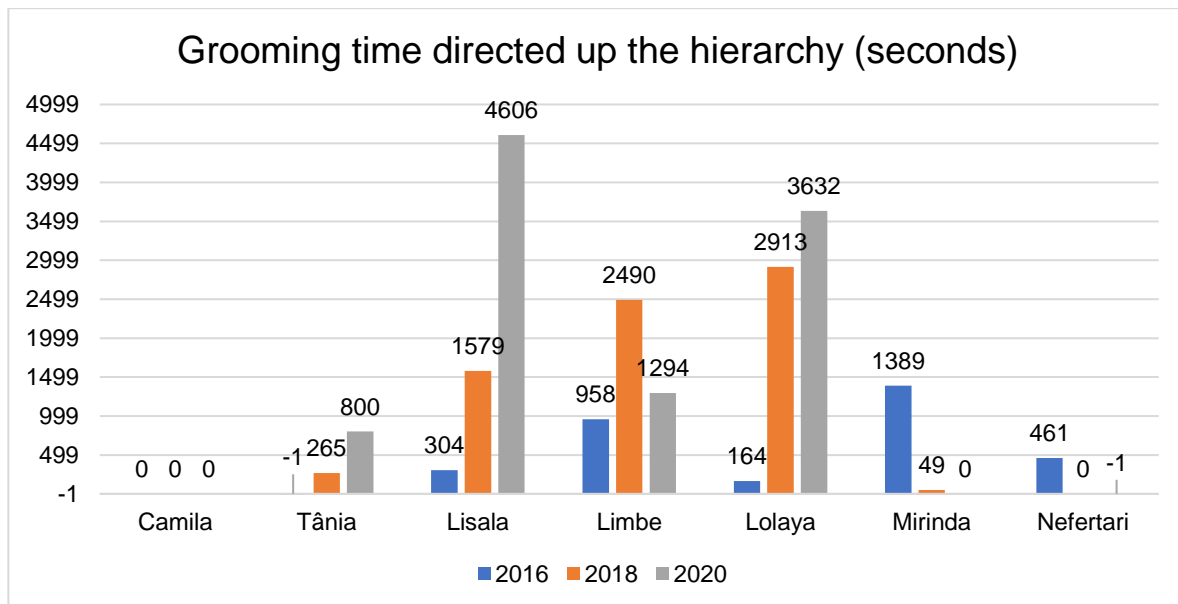

Figure A16: Grooming time directed up the hierarchy by each female [2016, 2018 and 2020; a negative value (-1) was attributed to unsampled or absent females].

Table A13: Grooming partnerships of each focal for 2016.

Females in 2016 (groomer)	Grooming partnerships (groomed)		
Camila	Lisala (25.8%)	Limbe (74.1%)	
Lisala	Camila (79.6%)	Limbe (17%)	Lolaya (3.4%)
Limbe	Camila (88.7%)	Lisala (11.2%)	
Lolaya	Lisala (6.5%)	Mirinda (87.5%)	Nefertari (5.9%)
Mirinda	Lolaya (19.2%)	Nefertari (80.8%)	
Nefertari	Mirinda (100%)		

Table A14: Grooming partnerships of each focal for 2018.

Females in 2018 (groomer)	Grooming partnerships (groomed)		
Camila	Tânia (80.1%)	Lisala (15%)	Limbe (4.9%)
Tânia	Camila (62.8%)	Lisala (8.5%)	Lolaya (28.7%)
Lisala	Camila (36.8%)	Tania (55.3%)	Lolaya (7.8%)
Limbe	Camila (56.7%)	Tânia (8%)	Lisala (35.3%)
Mirinda	Camila (100%)		
Lolaya	Tânia (80.1%)	Lisala (19.9%)	
Nefertari			

Table A15: DI scores and relative ranking (RR) scores of each female, for each period. Note for the "ND" values: In 2016 Tânia was not an adult female; Nefertari died 10 days after the end of observations in 2018 resulting in her absence in 2020.

Year / Individual	2016		2018		2020	
Dominance	DI score	RR score	DI score	RR score	DI score	RR score
Camila	1.00	1	1.00	1	1.00	1
Tânia	ND	ND	0.83	2	0.99	2
Lisala	0.80	2	0.67	3	0.60	3
Limbe	0.59	3	0.5	4	0.41	4
Mirinda	0.20	5	0.33	5	0	6
Nefertari	0.00	6	0	7	ND	ND
Lolaya	0.41	4	0.17	6	0	5

Table A16: Summary of the results from 2016, 2018 and 2020.

Summary table of results from 2016, 2018 and 2020		2016	2018	2020
H1	High-ranking females receive more grooming than low-ranking females	No	Yes	Yes
H2	Grooming directed up the hierarchy	Yes	Yes	Yes
H3	Grooming is more reciprocally traded between individuals closer in rank	No	No	No
H4	Reciprocity	Yes	Yes *	Yes
H5	Partner choice maintained	ND	Yes	Yes
H5	Grooming diversity index values	Low	Low	Low
H6	Grooming is traded for social tolerance (decrease in agonistic behaviour)	Yes	Yes	No
H6	Grooming is traded for social tolerance (Increase in ARE)	ND	ND	Yes

*Results from (Pereira *et al.*, 2019) suggested a decrease in the reciprocity levels in the 2018 period of data collection

Annex B

Example of the used focal sampling datasheet

Focal Sampling

Table A17 Example of the datasheet used for the focal sampling*.*

Time	Focal activity	Arms reach (App/Lv)	Proximity (J/Lv)	ID	Interacções	VOCS

Annex C

Ethogram

I. Maintenance behaviours:

Feeding, foraging, predation: The animal is engaged in any activity directly related to acquiring or ingesting food or fluid.

Locomotion: The animal moves between locations (from one place to another) by scooting, walking, running, climbing or swinging. Includes being carried (i.e., an infant clinging to its mother).

Sleeping: The animal is not moving; it may be lying or sitting, with its eyes closed for more than 50 seconds.

Stationary (resting, watching): The animal is not moving; it may be lying, sitting or standing. Non-locomotor movements are included (e.g., changing from sitting to lying). The animal may be asleep, or it may be alertly watching or listening. No social interactions happen.

Autogrooming: Animal picks through or examines its own pelage or skin (excluding the anogenital region) using fingers, lips or teeth.

II. Affiliative behaviours:

Allogrooming: animal picks through or examines the pelage or skin (excluding the anogenital region) of another animal using fingers, lips or teeth.

Ask to be groomed: Initiator ostensibly exhibits a part of its body to the recipient, very close to him, trying to start a grooming session.

Presentation: initiator orients its hindquarters towards the recipient, bending at least one knee, even if slightly, and looks over the shoulder at the recipient at least once for any length of time.

Touching or tugging: initiator touches gently or tuggs the fur or other body parts (other than the anogenital region) of the recipient outside the context of aggression or social play.

Following: initiator walks less than one meter behind the (walking) recipient for at least one meter, outside the context of social play or aggression.

Play-fight: initiator is engaged in fight-like activities with wrestling behaviours. The situation, however, is exploratory and not aggressive.

Play-chasing: initiator simulates to chase the recipient, and the recipient simulates to run from him.

Hug: initiator puts its harms around the recipient's body.

Examining anogenital region: the animal looks at, sniffs or touches the anogenital region of the recipient.

Invite to anogenital region examination: Initiator exhibits its anogenital region to the recipient, possibly standing bipedally, trying to provoke a reaction.

Attempting to mount, unsuccessfully: the animal approaches another individual from behind, such that both are oriented in the same direction, and places its hands on the recipients' pelvis or lower back but does not, or cannot, proceed to a mount (see bellow), for any reason.

Mounting, successfully: genital-genital contact is made while the pair is arranged such that the initiator's abdomen is oriented towards the recipient's dorsum and both are facing the same direction. The animal may stand bipedally behind another, with its pelvis oriented to the recipient and its hands on the recipient's pelvis or lower back. May happen in both female-female or male-male dyads.

Resisting to mount: the initiator of the behaviour was recipient of a mounting but successfully prevented the intromission by moving away, twisting or pushing the animal attempting to mount it.

Pelvic thrusting: the animal repeatedly thrusts its pelvic region during a mount.

Intromission: the male appears to insert his penis into the recipient's vagina.

Ejaculation: the male appears to ejaculate. The animal may stop pelvic thrusting, tightens its grip on the recipient and shudders briefly. Semen may be seen on the recipient's perineum afterwards.

III. Agonistic behaviour:

Yawning (with head-tilt): Prolonged yawn. The head tilts back such that the animal is looking straight up, or nearly so. The mouth is opened so that the teeth are exposed (at least the premolars).

Head-bobbing: The initiator faces the recipient, mouth closed, and jerks its head downward with the crest usually raised. Sometimes, simultaneously. the animal slaps the ground.

Chasing: The animal rapidly pursues (running, not walking) another animal who is avoiding the initiator.

Pushing, hitting, grabbing: The animal uses its hands or feet for forceful contact aggression.

Biting with force: The animal bites another individual with sufficient force that the recipient screams or otherwise gives an indication of discomfort.

Fight: Initiator physically and systematically attacks the recipient. It may take the form of biting, pushing, slapping, etc.

Agonistic aiding: The animal goes to the aid of the recipient, who is involved in an agonistic interaction with a third animal. The recipient may have been either the aggressor or the victim of the original interaction. The aiding animal must direct some aggressive behaviour towards the recipient's opponent.

Objects supplant: Initiator takes the object that the recipient is holding from him.

Location supplant: Initiator moves to the same place where the recipient is. When doing this, the recipient "gives up" its location and moves away.

Food supplant: Initiator takes recipient's food.

IV. Other behaviours

Masturbating: the animal repeatedly presses or rubs its genitals (penis; clitoris, vagina) with its digits or an object. May reach orgasm.

Coprophagy: Animal consumes its own faeces.

R/R: Regurgitation and re-ingestion of food.

Stereotypical behaviours associated with paths: The animal walks on the same path, systematically and repeatedly, without any obvious reason.

Stereotypical behaviours associated with body positions: repeated body movements, with no obvious reason (e.g., turning the head).