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The Pegasus Review: UCF Undergraduate Research Journal (URJ)

Volume 10 | Issue 1 Article 5

2019

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Vol. 10.1: 35-46

URJ

THE PEGASUS REVIEW:
UNIVERSITY OF CENTRAL FLORIDA
UNDERGRADUATE RESEARCH JOURNAL

Published
October 29, 2018

The Effect of Social Hierarchy on Behavior in *Cercopithecus petaurista*

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ABSTRACT: The social group hierarchy of three captive *C. petaurista* specimens was monitored and determined by observing agnostic fights, aggression, and allogrooming incidents. This social group was monitored from May to August in 2017 for 60.5 observation hours total as a continuation of a previous study conducted in spring of 2017. The study took place at the Central Florida Zoo and Botanical Gardens. All observations were recorded on template sheets with the location of each individual noted on a 6x6 grid representing the enclosure. A new sheet was used for each 15-minute increment during observation periods. It was concluded that agnostic fight outcomes were influenced by social hierarchy, with more dominant individuals consistently winning encounters with less dominant individuals. It was also notable how the dominant male would step in to help settle agnostic fights, enforcing the hierarchy among less dominant individuals. Allogrooming also was influenced by hierarchy. Grooming incidents among the observed specimens followed the Seyfarth model, meaning that grooming tended to take place among individuals of adjacent rank.

KEYWORDS: animal behavior; primates; social hierarchy; allogrooming; Seyfarth model; *Cercopithecus petaurista*; lesser spot-nosed guenon

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INTRODUCTION

The order *Primates* is comprised of individuals that share morphological traits such as front facing eyes, opposable thumbs, and a more complex brain. Species within this order also tend to be highly social. In many cases, individuals spend their lives living in social groups. The general structure of these groups varies from species to species with different ratios of males and females observed within a community. The benefits of this social structure include a greater ability to dominate local resources through group foraging and a greater ability to defend against predators (Majolo et al. 2008). One species that is observed to live in a social structure is *Cercopithecus petaurista* or Lesser Spot-Nosed Guenon which features a polygynous hierarchy, with one dominant male and several females. The male is typically the most dominant individual within the social group, maintaining order and defending against predators (O'Neil 2012). The females of the group also fall under a hierarchy, but are almost always hold a social status below the male.

In studies on *C. petaurista* and other species under the same genus, it appears that the position of a female in the hierarchy can be determined by observing behaviors in grooming and aggression incidents. Studies such as Struhsaker's on *C. aethiops* and Cheney's on various Cercopithecus species observed that the social rank of female members of a community had direct influence over the competition over grooming with male partners (Struhsaker 1967). It is also important to note that individuals on the lower end of the social hierarchy are more likely to groom other members of the community than they are to receive grooming since individuals at the top of the hierarchy have to maintain an identity of being a high-ranking member of society (Chiarelli 1980). This phenomenon has a direct influence on the overall health of individuals across the social hierarchy. Those holding lower social statuses are at a higher risk for several health issues since receiving grooming has a positive effect on immune system strength (Caruso 2016). When analyzing the immune cells of monkeys at different positions within a hierarchy, individuals towards the top of the hierarchy had a higher T-cell count and, as a result, were better equipped to respond to disease (Snyder-Mackler et al 2016). Struhsaker also notes that aggression over special positioning and food resources was commonplace when both resources were in limitless supply. Dominance can be traced through which individual successfully won these resources in agonistic fights.

The goal of this study is to expand upon these observations on the social dynamics within the *Cercopithecus* genus to determine if this behavioral trend persists within a community living in captivity. Accordingly, agonistic fights and social grooming behavior were observed to determine if they are both influenced by the social rank of an individual and if they can help determine the social hierarchy of a captive *C. petaurista* community. This information will help increase the quality of care for *C. petaurista* communities in captivity since understanding the full effect hierarchy status holds over individuals allows keepers and management to deal with the various issues faced by community members at different social ranks.

BACKGROUND

The Lesser Spot Nosed Guenon belongs to the *Cercopithcinae* subfamily. This subfamily is defined as old world monkeys found within Sub-Saharan Africa characterized by a simple stomach and the presence of cheek pouches used to temporarily store food. These pouches can hold the equivalent of a stomach load of food and have been observed to be used to hoard food from conspecifics (Buzzard 2006). This adaptation benefits the individual since the use of cheek pouches significantly reduces time spent in areas of high competition or predation risk. The *Cercopithcinae* subfamily shares an omnivorous diet consisting of fruit, insects, and leaves. When foraging, groups of *Cercopithcinae* assume a dispersed spacial positioning with the most profitable positions being at the edge of the group. Dominant individuals are often seen claiming the densest food patches and defending them from less dominant members of the group (Hirsch 2007). Another trait of the *Cercopithcinae* subfamily is a high degree of sexual dimorphism. In the case of C. petaurista, females weigh 66% less than their male counterparts (Kingdon 2003).

C. petaurista or Lesser Spot-Nosed Guenon is defined by the large white spot on this species' nose. *C. petaurista* is generally 0.91 to 1.22 m long and weighing 2.72-3.62 kg on average (Central Florida Zoo). The lifespan of this species is around 20-30 years in length. There are two subspecies of *C. petaurista* isolated by a river that splits the territory the species occupies along the coast of Western sub-Saharan Africa. (Kingdon 2003). Within this territory, this species can be found in terrestrial ecosystems such as primary forests, secondary forests, farm clearings, and successional forests. It is diurnal and moves quadrapedally through the lower strata of

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the forest canopy in its natural habitat (Central Florida Zoo). Mating within communities of *C. petaurista* is polygamous with communities consisting of anywhere from 10-40 individuals. Sometimes, these groups can be interspecific among other species of *Cercopithecus* (San Diego Zoo). Females have been observed to engage in "presenting" to display to males their sexual receptivity. Presenting behavior is a visual signal communicated when an individual raises their posterior in the air towards another individual. It can also be used as a greeting or submissive display (Morris 2006). Mothers typically give birth to and care for one infant. Cooperative breeding, a form of parental care where individuals that are not directly related to offspring aid in rearing them, is commonly seen in this species among the females of a community. Natal dispersal is often seen in the wild when male youth reach adolescence. These males will either become the head of their own communities or become a roaming male. Roaming males can either live in solitude or as a part of a bachelor group (Central Florida Zoo).

Figure 1: Social Grooming observed in C. petarurista.

As a highly social species, communication is complex and highly developed among *C. petaurista*. This species is mostly reliant on visual communication through complex head movements. The importance of this mode of communication can be seen through the adaptation of the white spotted nose, which allows this species to visualize head movements across a distance in their forest habitat (Zoo Miami 2017). Facial expressions and posture are also used as a form of visual communication. They are often incorporated into agonistic threat displays in the forms of bared teeth, an open mouth, and staring with raised brows (Morris 2006). Auditory communication is also present among this species through chirping and sneeze-like vocalizations. The sneeze call is used as an alarm call to alert conspecifics about the presence of aerial predators. A purring alarm call has also been observed among C. petaurista to distract predators, thus facilitating the escape and survival of other community members (San Diego Zoo).

As a primate, social grooming, as seen in Figure 1, is another key aspect of social dynamics within *C. petaurista*. Grooming in wild populations has been observed to be linked to social status. In his paper, Robert Seyfarth models this dynamic based on wild social groups of old world monkeys. According to the Seyfarth model, female members of adjacent ranks within a social hierarchy are the most likely pair to be grooming partners due to a desire to groom those who hold a higher social status to gain access to some of their privileges. Grooming with top ranking partners is limited by competition with other members of a group for these high-ranking grooming partners (Seyfarth 1977).

MATERIALS AND METHODS

To observe the social hierarchy of *C. petaurista* a group consisting of two females and one male was monitored in an enclosure at the Central Florida Zoo. The dominant male, named Timbi, was born in 2003. The eldest female, Mama (depicted in Figure 1.2 below), was born in 1999. The younger female, Tumani, was born in 2001. Both Mama and Timbi had a section of their tail removed for health reasons. There are a few notable relationships within this group. Timbi and Mama were a former mating pair, while Timbi and Tumani are half siblings on their father's side.

Figure 1.2: Social Grooming observed in C. Petaurista.

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It is important to note that this study is a direct continuation of another study conducted on the same subjects by UCF student researcher Ryan Domitz. In his study, he observed hierarchy in terms of grooming solicitation and determined how the subjects spent their time on average. During his observations, Domitz observed a change within the social hierarchy. On March 26th, 2017, there was an aggression incident between Tumani and Mama within the enclosure den. Mama had to be removed from the exhibit after losing the confrontation with Tumani and needing medical care. When Mama was reintroduced back into the enclosure, Tumani had taken her place on the social hierarchy leaving Mama with the lowest social status of the three subjects. This change in social status led to an increase in agonistic behavior from Timbi and Tumani directed at Mama. This shift persisted throughout the remainder of this student's study with no signs of a reversal back to the status quo before the aggression incident leaving the hierarchy as Timbi > Tumani > Mama when this study commenced.

The enclosure at the Central Florida Zoo is a fenced in box shaped area with dimensions of 9.144 x 7.62 x 3.353 meters. Three of the walls are held up by cement blocks with the front and most of the roof of the enclosure are fenced in. There is also a fenced in window built into the center of the back wall. On the left wall of the enclosure, there are two enclosure doors leading into a neighboring den where the Guenons are moved when the enclosure is cleaned or overnight when the zoo is closed. The guenons are also moved into the den when the outside temperature reaches below 4.44ºC. Within the confines of the enclosure walls, there are several tree-like structures with branches that stretch across the enclosure above the ground. The back half of the enclosure is covered with a closed roof and features a small treehouse for the guenons to retreat to for privacy. Enrichment is occasionally placed around the enclosure before the three individuals are released from the den in the morning or after enclosure cleaning. This enrichment varied from new foods like full branches and nuts to additional rope structures and ladders placed in various locations around the enclosure. Outside the enclosure, there is a Brown Lemur (*Eulemur fulvus*) exhibit to the left, a Red Ruffed Lemur (*Varecia rubra*) exhibit to the right, and a Ring-Tailed Lemur (*Lemur catta*) exhibit directly across from the Guenon enclosure. The Brown Lemur and Ring Tailed Lemur were relatively quiet and rarely produced vocalizations that produced a reaction from the guenons. The Red Ruffed Lemur, however, produced loud snarling and squeaking vocalizations at varying times each day that sometimes produced a response from the guenons. Inside the enclosure, the guenons had direct contact with Eastern Grey Squirrels (*Sciurus carolinensis*) and House Sparrows (*Passer domesticus*) as these animals were small enough to slip through the bars and enter the enclosure. This was commonplace since these animals were attracted to the primate biscuits scattered throughout the exhibit.

To observe the social hierarchy among these three individuals, behavioral observations were made over 2 to 4 hour periods at random time intervals, three times a week for a total of 60.5 hours (between May 22, 2017 and August 28, 2017). Observations took place at the front of the enclosure in full view of the animals. Zoo guests were also present during observations with varying degrees of crowd size and noise levels. It is also notable that the guenons were sent into the den around noon for enclosure cleaning and feeding which may have modified behavior. A template was used to record notes during observation sessions. A new template sheet was used for each 15-minute period during observations. A 6x6 grid was on the top of each sheet to take down the locations of each specimen at the beginning of each 15-minute time block. The locations of enrichment and disputed territory were also marked down on the grid. Below the grid, behavioral observations were recorded. In a column next to the observations, notes on agonistic fights were recorded keeping track of which individual won the encounter. "Winning" an encounter was defined by either successfully taking territory, food, or another resource or receiving a submissive gesture or facial expression from another individual. The submissive gestures recorded in these cases were either a presenting gesture or the baring of teeth in response to aggression. Social grooming was also recorded, taking note who received the grooming and the length of the grooming if it lasted more than 1 minute. This data was analyzed by counting the number of times each specimen achieved victory in agonistic encounters. The number of grooming incidents was also counted, taking note of the direction of each grooming observed and the average length of grooming time between each possible pair.

RESULTS

Table 1 (see appendix) lists the number of times each individual "won" an agnostic encounter against another member of the community. Figure 2 (see appendix) graphs these observations to compare how many times each member dominated a particular individual.

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Table 2 (see appendix) lists out observations on social grooming. The number of times grooming was observed is listed next to each possible pairing along with total grooming time and average grooming time observed in that particular pair. Figures 3 and 4 (see appendix) graph out this data to compare total time and number of observations for each grooming pair. Figure 3 considers each possible combination of groomers and receivers as separate pairs while Figure 4 solely looks at combinations of individuals. Figures 5 (see appendix) compares the average grooming times for each combination of groomer and receiver. Figure 6 (see appendix) compares the grooming time received for each individual.

Other notable observations

Timbi would enforce the hierarchy and step in to enforce it during agnostic encounters. Agnostic encounters were often sparked by food. Timbi was the only individual observed giving alarm calls. Consistent level of reciprocal grooming observed more often between the two females than any other grooming pair.

DISCUSSION

Based on the data it appears that the hierarchy change observed in March of 2017 remains within this group. Table 1 and Figure 3 both back this up by clearly showing that Timbi, the dominant male, expressed authority over both Mama and Tumani through the comparatively high number of dominances in agonistic encounters observed. Tumani's position in the middle of the social hierarchy can be seen through her high number of dominances over Mama but only one successful challenge over Timbi. Mama's position at the bottom of the hierarchy is clear since she was never observed to have dominated Timbi and was only successful twice in dominating Tumani. The linear hierarchy seen through the data is also consistent with behaviors observed in the wild since linear hierarchies are isolated to simians in the *Cercopithcinae* subfamily, which includes this species (Welker 1985).

After viewing the hierarchy in terms of dominance, it is also notable that Timbi would step in to assist Tumani in dominating Mama on a consistent basis. This is primate behavior seen in the wild where the entire group works together to enforce a hierarchy through gestures and expressions to influence the social status of an individual throughout their life (Lewis et al. 2013). It is possible that the times Timbi stepped in to enforce the hierarchy were an attempt to prevent the threat displays between Mama and Tumani from escalating into a physical confrontation. Such de-escalation behavior has been documented as an important role of the dominant male in wild *Cercopithecus* species, in which the male uses subtle agnostic expressions to prevent fights and keep order within the group (O'Neil 2012). There were two documented cases of Mama expressing dominance over Tumani, however, they did not appear to be escalating beyond threat displays like the cases where Timbi stepped in to help Tumani dominate Mama.

The dominant male's role as the leader and protector of the group was also observed in alarm call behavior. This alarm call was rarely observed during the observation period. It was only recorded twice and were responses to loud thunder in the area. Timbi was the one giving the alarm call for both instances. This observation is consistent with observations made on *Cercopithecus* species in the wild. According to a study conducted by Papworth on *Cercopithecus mitus stuhlmanni,* the males within the group were the ones to deliver the alarm call. Papworth suggests that this is because males undergo natal dispersal as adolescence and afterwards need to maintain dominance over their new social group. Even though being the producer of the alarm call puts the dominant male at greater risk of predation, it is in his biological interest to protect his group. If he were to lose his group in a predator attack, the male would have to either reestablish himself as the dominant male of a different group or directly compete with another dominant male for control of a group (Papworth et al. 2008).

Based on my observations, it seems that many of these aggression incidents were sparked by food. Timbi was particularly aggressive about food, chasing around Mama and Tumani if they found a food source he was not aware of. Tumani also instigated agnostic fights over food but only with Mama, following the social hierarchy. This observation is consistent with the observations documented by Hirsch on foraging behavior and spacial positioning in *Cercopithecus* with the more dominant individuals claiming desired food patches (Hirsch 2007). Another observation on foraging that was consistent with this model was seen in the positioning of the three guenons when eating. It was commonplace to see all three eating in opposite corners of the enclosure, which follows from the predicted dispersal of individuals preferring the edge of the group.

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During these agnostic encounters, however, it was not observed that any of the specimens used their cheek pouches to secure food from their aggressors as seen in other guenon species. This apparent abnormality runs consistent with a study on cheek pouch usage conducted by Buzzard. The spot-nosed guenon was the only species where an increase in cheek pouch usage was not observed with the introduction of more competition for food. This effect even included direct competition with Diana monkeys, a particularly aggressive species of *Cercopithecus* (Buzzard 2006). This trend was explained through the foraging and antipredator behaviors of *C. petaurista.* Compared to other species under *Cercopithecus, C. petaurista* consumes less fruit and is more of a folivore. In Buzzard's study guenon species that were primarily frugivores had the highest degree of cheek pouch usage than those that were not. When looking at antipredator behavior, *C. petaurista* uses crypsis to hide amongst the dense foliage of its surrounding environment. Other species of *Cercopithecus* rely more on group defense among multiple species. Group defense may, in turn, lead to a higher use of cheek pouches because of the more aggressive antipredator defense strategy that incentivizes movement over staying in one space and increased competition because of the dependence on colonies of other species for a group defense and the benefits of the dilution effect in a larger group of individuals (Buzzard 2006). This may also be the reason why there was a significant amount of aggression surrounding food since competition for this species in the wild is primarily intraspecific instead of interspecific.

The data also shows that social hierarchy holds influence over social grooming. When looking at each specimen, figure 5 shows that each individual spent more time on average grooming an individual with a higher social status than they did receiving grooming from that same individual. For example, between Tumani and Mama, Mama spent 10.625 minutes on average grooming Tumani while only receiving 7.53 minutes of grooming. Another trend to note is that number of observations on grooming received parallels the rank along the social hierarchy. Timbi was observed to receive the most grooming at 37 times total, followed by Tumani at 24 times total. Mama was observed to receive grooming the least amount of times at 17 times total. These observations are consistent with a model of grooming developed by Robert Seyfarth, which predicts female members of adjacent ranks within a social hierarchy are more likely to be grooming partners (Seyfarth 1977). This pattern occurs because members of a community desire to groom with those that hold a higher social status to gain access to some of their privileges, but at the same time, such a patter complicates with competition for these high-ranking grooming partners. This combination of factors makes grooming with the next adjacent rank the most likely and socially reinforced grooming option (Tiddi 2012). While the results of testing this model have been mixed, there is substantial evidence that the model works well in species with a strong, linear hierarchy (a trait of the *Cercopithcinae* subfamily) and that there is a connection between social status, being a desirable grooming partner, and competition over grooming partners (Vila 2015). One result of this model is that since higher social rank makes a group member a more desirable grooming partner, a highest-ranking member like Timbi receives more grooming opportunities than those lower in rank. The number of times grooming was received continued to reflect the hierarchy when looking at Tumani and Mama since desirability as a partner decreases along with social status.

Another way the data lines up with the Seyfarth Model can be seen in Figure 5. While Mama and Tumani groomed the lowest number of observed times, they groomed for a longer average time than any other pair. On more than one occasion, Tumani ended grooming between Mama and Timbi with agonistic behaviors such as chasing Mama away from Timbi or carrying out a threat display using agonistic facial expressions and posture. To further support the Seyfarth Model in action, no other grooming pair was observed to be interrupted and separated through dominance challenges. Since the only other grooming pairs possible are made up of individuals of adjacent rank, this result is consistent the Seyfarth Model.

According to Figure 6, both Tumani and Mama received grooming for a longer amount of time than Timbi. This observation is due to a higher level of reciprocal grooming between females of the *Cercopithcinae* subfamily (Vila 2015). Properties of the Seyfarth Model may have exaggerated this trend further since Tumani and Mama were both the only two females in the group and adjacent in rank.

While most of the grooming data seems to directly follow the hierarchy, two pieces of data conflict with the rest. Figure 6 shows that the amount of time grooming was received on average runs opposite to the dominance hierarchy. Based on the literature and the data, I believe that this is the result of several different factors at work.

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First was the high level of reciprocal grooming between Mama and Tumani. Whenever Tumani would solicit grooming from Mama, it was almost always a case of reciprocal grooming. Timbi, in comparison, participated in a very low degree of reciprocal grooming possibly encouraging Mama to groom Tumani more often since she was more likely to receive grooming in return. Second was the effects of the dominance hierarchy through the lens of the Seyfarth Model. For the most part, Mama was limited to grooming with Tumani due to social rank. In the times where Mama would groom with Timbi, Tumani would put on a threat display to challenge Mama. Since Mama could not challenge Tumani back, these grooming sessions would usually end with Mama running away in submissive manner. Because of these aggressive encounters between Mama and Tumani in particular, Tumani would groom Mama as a means of reconciliation (Puga-Gonzalez et al. 2009).

CONCLUSION

Understanding social hierarchies in nature is an important endeavor for institutions that raise animals in captivity. Knowing the composition of social groups in the wild will help reduce and even prevent aggression events within exhibits since some communities function best with a certain sex ratio such as *C. petaurista.* It is also beneficial to understand the source of aggression incidents in certain species to understand how to reduce them. For example, in *C. petaurista,* food sparks many aggression incidents because they are behaviorally adapted for intraspecific competition because of the species' lifestyle in the wild. Being able to determine the social status of an animal is another important ability in caring for captive animals. Dominant individuals will often restrict submissive individuals from important resources such as food or shelter (Rees 2011). By being able to determine which animal has a lower social status, care can be adapted to ensure that particular animal is receiving the resources it needs to remain healthy. By way of example, the keepers at the Central Florida Zoo apply this knowledge in the care of Mama by slipping her extra food when the more dominant individuals are not aware. The results of this study have shown that agonistic fights and social grooming behavior are both influenced by social rank and can help determine the social hierarchy of a *C. petaurista* community. The highest-ranking member should have the most victories in agonistic fights with every member of a group and receive more individual grooming sessions as the most desirable grooming partner. Lower ranking members are dominated by all other members of a group in agonistic fights and receive the least grooming sessions from other members. To expand on these results, repeating this study among a larger community of *C. petaurista* would help solidify the relevance of the Seyfarth Model and investigate the full extent of the effect reciprocal grooming has within the female population of a group over average grooming length. Such a study could determine if the trends observed within the data persist in larger communities of *C. petaurista* or if the small group number of this study skewed the results by causing a change in behavior from what is expressed outside captivity. Wild populations of *C. petaurista* have more female members, have male-male competition as dispersed males fight group leaders for their position on the hierarchy, and polyspecific interactions with neighboring arboreal primate populations (Buzzard 2010).

ACKNOWLEDGMENTS

I would like to thank Frank Logiudice, Jonathan Napier, the UCF Biology Department, and the Central Florida Zoo for making this study possible.

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Table 1: Dominations observed for each individual

	Dominates Timbi	Dominates Mama	Dominates Tumani
Timbi	N/A	37	18
Mama	0	N/A	2
Tumani	1	40	N/A

Table 2: Grooming observed and length of grooming in minutes

	Times observed	Total Time (Min)	Average Time
Timbi > Mama	2	2	1
Timbi > Tumani	16	35	2.1875
Mama > Timbi	23	132	5.739130435
Mama > Tumani	8	85	10.625
Tumani > Timbi	14	38	2.714285714
Tumani > Mama	15	113	7.533333333

Figure 2: Graph comparing number of dominations observed through agonistic encounters

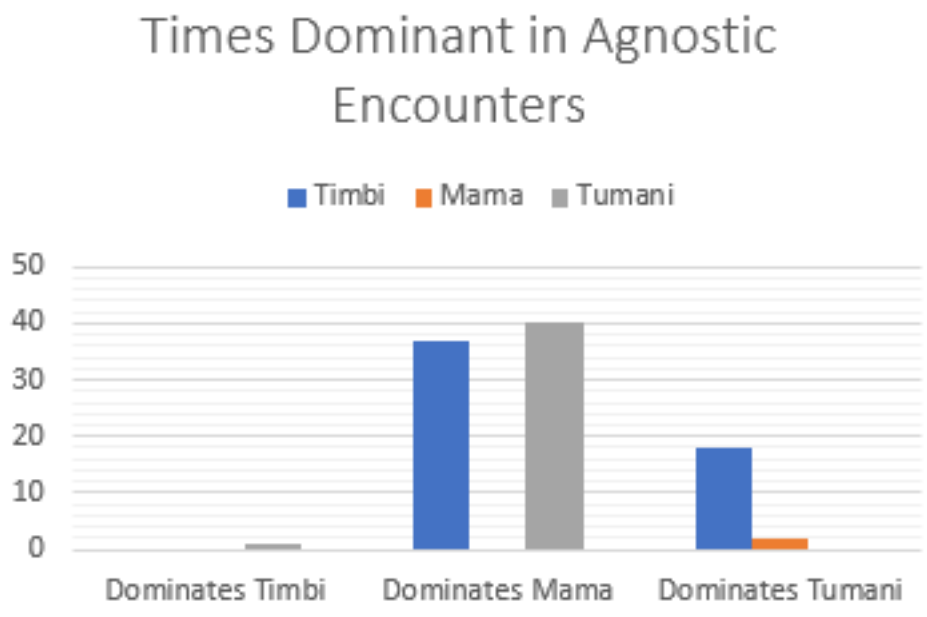

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Figure 3: Graph comparing groomings observed and grooming length for each possible grooming pair

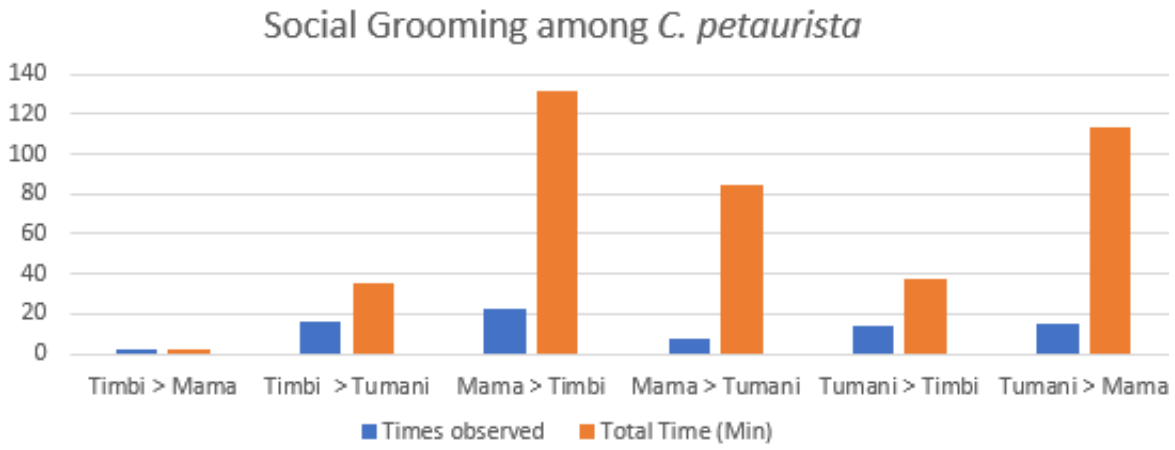

Figure 4: Observations and average grooming Length by Grooming Pair

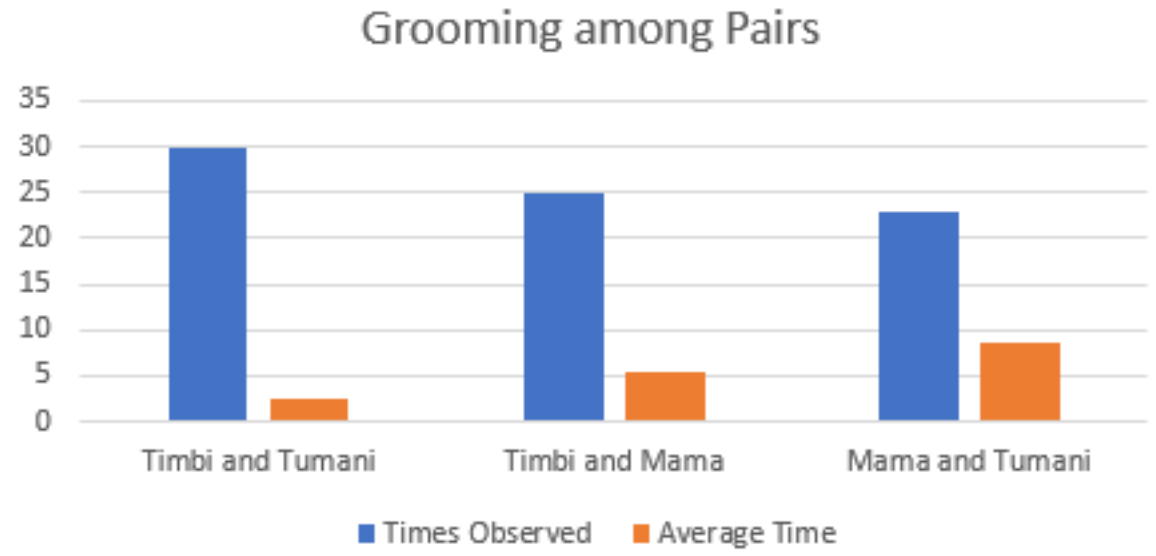

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Figure 5: Graph comparing average grooming times among grooming pairs

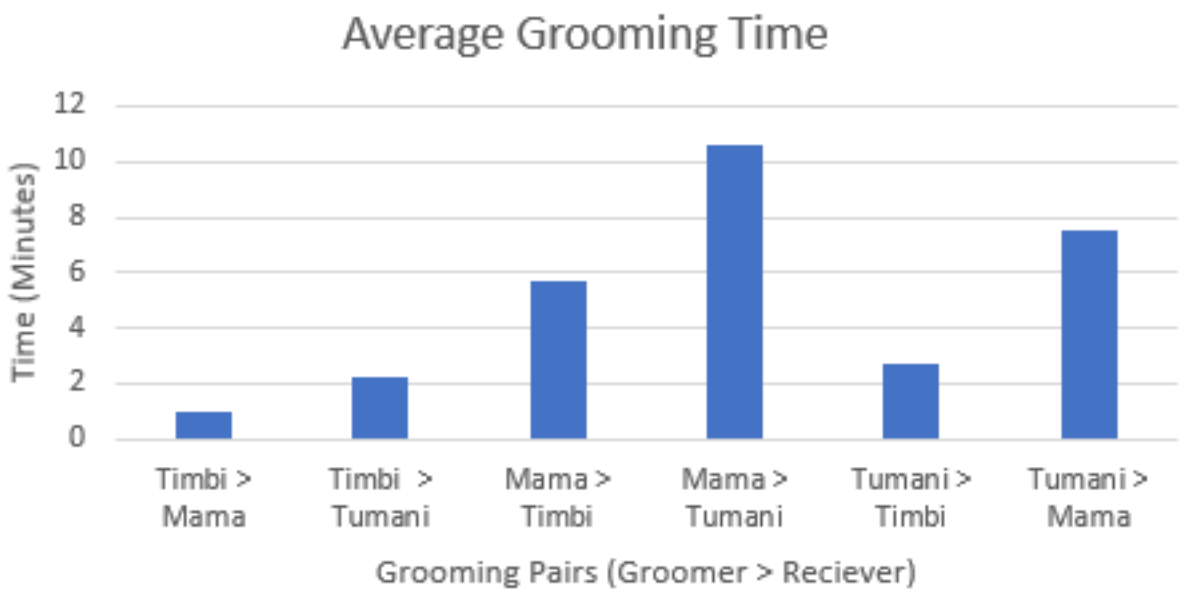
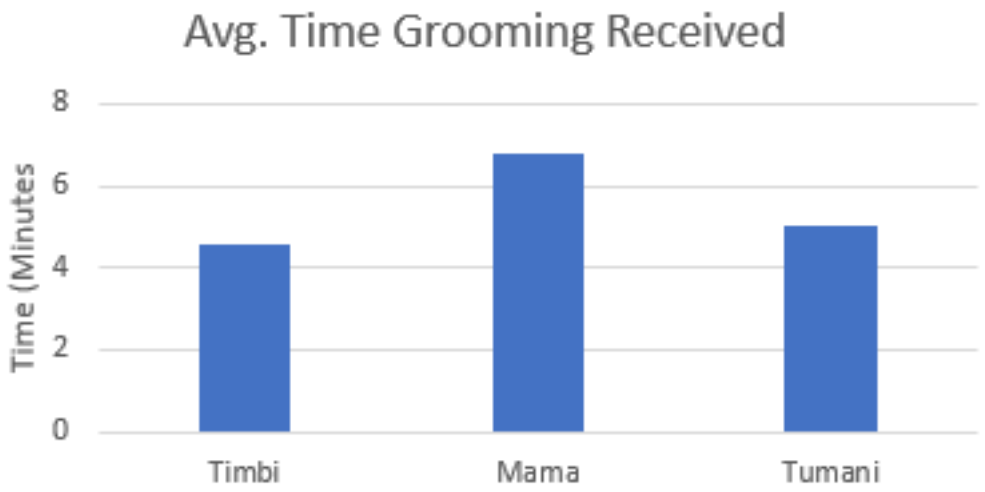


Figure 6: Graph depicting total average time an individual received grooming



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