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THE INFLUENCE OF HIERARCHY STEEPNESS ON COOPERATION: A COMPARISON BETWEEN CAPTIVE JAPANESE MACAQUES AND BLACK-HANDED SPIDER MONKEYS

by

Sean Draxler

A Thesis Submitted in
Partial Fulfillment of the
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December 2017

ABSTRACT

THE INFLUENCE OF HIERARCHY STEEPNESS ON COOPERATION: A COMPARISON BETWEEN CAPTIVE JAPANESE MACAQUES AND BLACK-HANDED SPIDER MONKEYS

by

Sean Draxler

The University of Wisconsin-Milwaukee, 2017
Under the Supervision of Professor Trudy Turner

Non-human primates often live in social groups that form hierarchies, which can be either egalitarian or despotic. Despotic non-human primate groups are characterized by the ability of dominant members to frequently win dyadic conflicts against subordinates, and egalitarian primate groups are characterized by an unclear ranking of dominance. Non-human primates will often cooperate with each other within their social groups. Cooperation can be defined as the sharing of food, grooming, and formation of alliances. In a comparative study between bonobos (*Pan paniscus)* and chimpanzees (*Pan troglodytes)*, it was suggested that hierarchy steepness is a good predictor of sharing between unrelated individuals, and sharing was directed more unilaterally from subordinate to dominant among the more despotic bonobos (Jaeggi, Stevens, & Schaik, 2010). In contrast, another study found that the introduction of shareable resources and induced cooperation can also reinforce rank between members and members will aggregate into groups of similar rank (Pansini, 2011).

The goal of this research is to further elucidate the role that hierarchies play in forming reciprocal relationships between members by comparing two captive populations. The hypothesis of this thesis is that if the hierarchy of a primate group is despotic then there will be less cooperation between individuals, and if a primate group is egalitarian then there will be more cooperation between members.

A group of despotic Japanese macaques (*Macaca fuscata*) was compared to the more egalitarian black-handed spider monkeys (*Ateles geoffroyi*). This study observed the grooming patterns, spatial associations, agnostic behaviors, and transfer of food between individuals and tested to see if there was evidence of reciprocity. The investigation also tested to see if exchanges of grooming and food were directed unilaterally from subordinate to dominant in both groups. It was expected that more despotic Japanese macaques would exchange food and grooming unilaterally towards rank, and that the more egalitarian black-handed spider monkey would provide food and grooming if they received food and grooming. It was found that there was no evidence for reciprocity or unilateral exchange of food and grooming in either primate group. Instead, it could be argued that while hierarchical steepness within a group can influence the flow of food and grooming, the environment also influences the exchanges of food and grooming between members. In environments in which members do not need to compete, there may be an absence of directionality in the exchange food and grooming.

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Chapter 1: Introduction

Primates are social creatures that form social groups that differ in size and organization. In many species cooperative behavior is currently observed in the form of sharing food, exchanging grooming, or coming to the aid of allies. Many species exhibit social hierarchies through dyadic encounters, which establish the priority of group members' access to food and mating opportunities (Strier, 2007). Hierarchies differ in proportion with the number of dyadic conflicts won by dominants. In steep (or despotic) hierarchies this proportion is higher (Fuentes, 2011; Sterck, Watts, & Schaik, 1997). In egalitarian groups this proportion is much lower and there is often no clear linear dominance in the relationships between individuals (Maestripieri, 2012).

The hierarchy of a primate social group impacts how cooperative behavior is expressed within the group. The purpose of this thesis is to examine the impact of hierarchy on cooperative behavior by comparing two primate species that have different hierarchies: Japanese macaques (*Macaca fuscata*), and black-handed spider monkeys (*Ateles geoffroyi*). Japanese macaques typically form despotic matrilineal hierarchies where females inherit their rank from their mothers (Thierry, 2011; Yamagiwa & Hill, 1998). In contrast, black-handed spider monkeys form more egalitarian groups where it is often difficult to determine dominance relationships between female conspecifics (Asensio et al., 2008).

The environment strongly influences the steepness of hierarchies because females organize themselves in response to the spatial and temporal distribution of food and predation (Fuentes, 2011). Groups in environments where access to food occurs in patches engage in

contest competition. Females in groups that engage in contest competition tend to form stronger bonds, which can lead to despotic hierarchies with a clear ranking of dominance between members (Sterck et al., 1997). When food patches are scattered and individuals compete against time rather than other individuals to access food (**scramble competition**) groups tend to exhibit weaker bonds between females, resulting in a more egalitarian hierarchy that lacks clear dominance relationships (Fuentes, 2011).

The relationship between hierarchical steepness and cooperation is not entirely straightforward. A recent study compares bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) to suggest that hierarchy steepness can be a good predictor of sharing between unrelated individuals (Jaeggi, Stevens, & Schaik, 2010). Among despotic bonobos, subordinates will give more often to dominants than dominants will give to subordinates (Jaeggi et al., 2010). In egalitarian chimpanzee groups the more dominant chimpanzees are more likely to share with lower ranked individuals (Jaeggi et al., 2010). The study suggests that cooperation in steeper hierarchies will be directed asymmetrically towards dominants, but cooperation in egalitarian groups will be more symmetric.

A study involving vervet monkeys (*Chlorocebus pygerythrus*) demonstrates that the introduction of shareable resources and induced cooperation can affect rank relations between members and that individuals will aggregate into subgroups of similar rank (Pansini, 2011). In this experiment, individuals need to cooperate with each other to gain access to a resource, but there is still competition between members because the resource is monopolizable. The study suggests that the introduction of shareable resources with induced cooperation can increase competition, leading to steeper hierarchies. The study also supports Wrangham's claim that affiliative bonds are naturally selected in environments that promote strong within-group competition, necessitating the need for allies (1980). The previous study involving chimpanzees and bonobos suggested that hierarchy is a good predictor of how members will cooperate within a group, but the study involving vervets suggests that the introduction of resources that require cooperation may lead to a steeper hierarchy. The two studies do not necessarily contradict each other, but they do suggest that the relationship between linearity and hierarchal steepness may not be linear.

Research Goals

The hypothesis of this thesis is that more despotic primate groups will exhibit less cooperation between individuals than egalitarian groups. This research will address the following questions: When compared to more despotic groups, do more egalitarian groups exhibit: 1) a higher proportion of reciprocal exchanges, 2) a lower proportion of unidirectional exchanges from subordinate members to dominant members, 3) a higher proportion of unilateral exchanges from dominant members to subordinate members, and 4) more cooperation between members that are closer in rank than between members that are further apart in rank?

Structure of the thesis

The study examined two captive non-human primate species that form hierarchies of different steepness. The first was a small group of four black-handed spider monkeys (*Ateles geoffroyi*) at the Racine zoo consisting of three females and one male. Spider monkeys form very fluid fission-fusion groups that are typically characterized by having weak female bonds and a more egalitarian hierarchy (Di Fiore et al., 2011). The second group is a small group of six

Japanese macaques (*Mucaca fuscata*) at the Milwaukee Zoo consisting of four females and two males. Japanese macaques typically form strict matrilineal hierarchies that are considered despotic (Berard, 1999; Tsuji & Sugiyama, 2014). The investigation observed grooming patterns, spatial associations (e. g., approaches and displacements), agnostic behaviors (dyadic conflicts), and the transfer of food between individuals.

The literature review of this thesis begins in the second chapter and will cover the behavior and ecology of the Japanese macaque followed by the behavior and ecology of the black-handed spider monkey. The third chapter will give a brief background on the theoretical perspective of socioecology and discuss how the environment influences the hierarchies of non-human primate groups. The fourth chapter will discuss how hierarchies influence cooperation within non-human primate groups. The fifth chapter will cover the methods and results of the study. The final chapter will outline conclusions drawn from the study.

Chapter 2: Ecology of Japanese Macaques and Black-Handed Spider Monkeys

Introduction

This chapter is broken up into two separate sections examining the ecology and behavior for the species observed in this investigation: Japanese Macaque and the black-handed spider monkey. Each species' section in this chapter will review four topics: 1) the taxonomy and lineage 2) morphology, 3) the unique habitat and environment that both primate species live in, and 4) the social-organizations and social structures of both primates.

The Behavior and Ecology of the Japanese Macaque (*Mucaca fuscata)*

Taxonomy

Macaques are a monophyletic group within the family *Cercopithecidae* and are in the tribe *Papionini* along with baboons and mandrills (Thierry, 2011; Thierry, Singh, & Kaumanns, 2004). The genus *Macaca* diverged from *Papionini* about 7 million years ago and radiated throughout Euroasia 5.5 million years ago (Thierry, 2011). The genus *Macaca* contains 22 species (figure 1) divided into 3 three lineages: the silneus-sylvanus lineage, sinica-artoides lineage, and the fascicularis lineage (Thierry et al., 2004). Speciation of the current extant lineages of *Macaca* occurred within the last 2 million years (Thierry et al., 2004). It is believed that the silneus-sylvanus lineage is the most ancient of the three

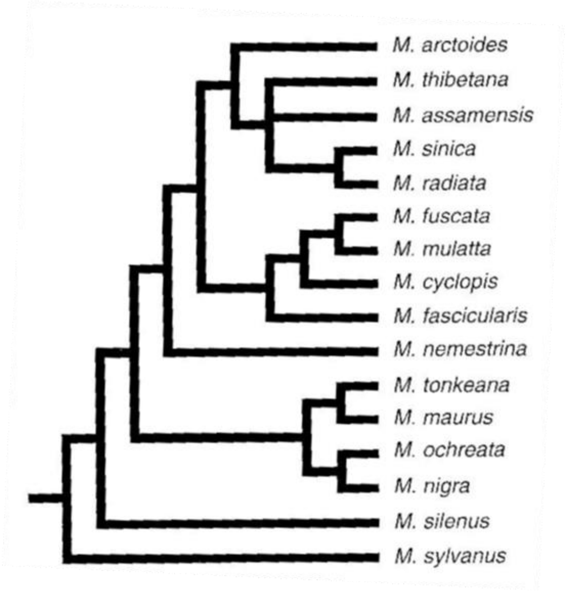


Figure 1: Phylogenetic tree of macaques showing the separate linages (Thierry et al., 2004, p. 9)

lineages. This is supported by the presence of the amino acid threonine within the 9th and 13th position of the hemoglobin beta chain within the silenus-sylvanus lineage, which is absent in the other two lineages (Fa, 1989). The Japanese macaque belongs to the fascicularis lineage which arose in Java during the glacial period and expanded northward, colonizing Taiwan through a land bridge that connected the islands of Sumatra, Kalimantan, and Java and is thought to be the last lineage to disperse (Fa, 1989; Thierry, 2011; Yamagiwa, 2010). Genetic analysis suggests that ancestral Japanese macaques migrated to Japan through a land bridge that connected North Korea and Japan about .43 to .60 MYA (Yamagiwa, 2010).

Morphology

Japanese macaques are terrestrial quadrupeds that do not display much suspensory behavior; however, they have are observed to use their hind-limbs for suspension while feeding (Fleagle, 1999b). All species of the genus *Macaca* possess cheek pouches that allow them to store food in their mouths (Thierry, 2011). Average weight for adult male Japanese macaques is 11.0 kg and adult females average 8.0 kg, so they are sexually dimorphic. Their dimorphism ratio is 0.32 and is calculated by taking the natural logarithm of the average male weight minus the average female weight (Sing & Sinha, 2004; Thierry, 2011, p. 234).

Males have larger canines and longer canine roots than females, but the size dimorphism is considered small for primates. The mean length of canine root length was 17.2 mm among males and 11.5 mm among females (Fukase, 2011). The average mandibular breadth is 46.1 mm for males and 40.1 mm for females, while the average mandibular length is 90.9mm for males and 78.2mm for females (Fukase, 2011, p. 610).

Both male and female adult macaques are characterized by a red face and possess a coat with a hue of brown to white depending on the time of the year (Fa, 1989). Japanese macaques molt yearly during the summer, and the summer coat begins as a darkish brown hue, which eventually greys out to a white hue during the winter and spring (Yamagiwa, 2010).

Female and male Japanese macaques mature at different rates, which is called bimaturism (Bercovitch & Harvey, 2004). The juvenile period for this species is demarcated by the development of a brown coat in summer starting at the age of 0.5 years and ends with sexual maturity (Yamagiwa, 2010). Male Japanese macaques begin to reach sexual maturity around the age of 5.5 years, which manifests with a reddening of the skin on their face, near the genitals, and on the posterior. Females begin to develop secondary sexual characteristics earlier, at 3.5 or 4 years, which manifest as teats, sexual skin, and the reddening of the face (Bercovitch & Harvey, 2004; Thierry, 2011; Yamagiwa, 2010). The first ovulation of a female begins at 3.5 years of age. Estrous lasts an average of 28.3 days and is not marked with sexual swellings, but the skin near the genitals changes color (Bercovitch & Harvey, 2004).

Japanese macaques live in a variety of diverse climates in Japan (Thierry, 2011; Thierry et al., 2004; Yamagiwa, 2010). They exhibit morphological adaptations involving thermal regulation to adapt to these diverse climates. Macaques possess peripheral tissues for heat insulation and populations further north also possess denser fur (Yamagiwa, 2010). Body size for Japanese macaques tends to be larger in localities with a lower average temperature (Yamagiwa, 2010). This increase in body size for Japanese macaques allows for greater fat storage in order to cope with the colder climates in northern Japan (Yamagiwa, 2010).

Ecology and Habitat

Japanese macaques are distributed throughout northern Japan from Shimokita Peninsula down to the southern Yakushima Islands and range between the latitudes of 30°N to 40°N (figure 2; Hanya, 2010; Thierry, 2011; Yamagiwa, 2010). Japan has seasonal changes in air temperature resulting in four distinct seasons: spring from March to May, summer from June to August, autumn from September to November, and winter from December to February (Tsuji, 2010). During the winter season, snow can reach as high as two meters in the north near Yakushima while the southern regions receive no snow (Agetsuma & Nakagawa, 1998; Tsuji, 2010). The macaques' ecological environments vary from sea coasts to more temperate mountain ranges. Temperatures within the subtropical evergreen forests in the south at Yakushima will rarely go below 10°C, but temperatures in the deciduous forests of Shiga heights in northern Japan can reach as low as -20°C (Agetsuma & Nakagawa, 1998; Hanya, 2010). The difference of habitats, climates, and distribution of resources among the various Japanese macaque groups result in differences of behavior and diet among the many macaque populations (Tsuji, 2010).

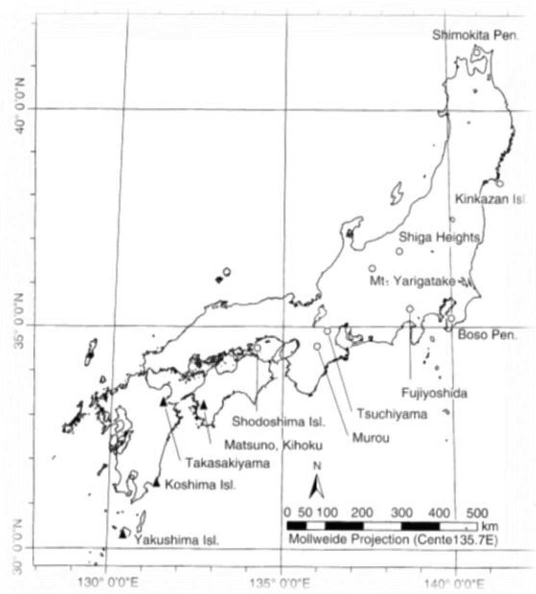


Figure 2: Visual of Japan ranging from the Shimokita Peninsula to the southern Yakushima Islands, ranging from 30 °n to 40°N (Hanya, 2010).

Japanese macaques exploit an eclectic selection of food including fruit, buds, bark, leaves, fungi, small vertebrates, and invertebrates (Tsuji, 2010). While macaques do have food preferences, they have a flexible diet and are not specialized to exploit any specific food resource. Macaques exploit only 19% of the plant species available at Kinkazan Island, 25.1% of the available plant species at Shiga heights, and 32.9% of the plant species at Yakushima (Tsuji, 2010, p. 103). The reasons for such differences has yet to be established but may be explained by climatic factors (Tsuji, 2010).

In the northern, cooler regions macaques are found to eat bark and dormant buds during the winter, but in the warmer regions, they spend more time eating fruits and flowers during the winter. In spring, Japanese macaques will eat young leaves and fruit (Hanya et al., 2006). During the summer, they will eat mature leaves along with fruits and seeds. The changes in food availability due to seasonal temperature change can also increase energetic cost, or caloric energy needed, of moving and can affect the amount of time that can be dedicated to eating.

A study comparing two groups of macaques that inhabit the two extremes within their range, Yakushima in the south and Kinkazan in the north, demonstrates a difference of feeding time and food quality between the groups (Agetsuma & Nakagawa, 1998). The optimal foraging model is posited to explain these differences, and it predicts that animals will increase time spent looking for high-yield foods such as fruit during periods of food abundance, and will decrease time spent moving while increasing feeding times during periods of food scarcity (Agetsuma & Nakagawa, 1998).

The study observes a decrease in moving time paired with an increase in feeding time for populations that are observed at both the Kinkazan and Yakushima field sites. More time is spent feeding on fruits during the July to November period at Kinkazan than at Yakushima. The study also finds a negative correlation between feeding time and the consumption of high-yield fruits, and a positive correlation between moving time and consumption of lower quality foods. The study suggests that an optimal foraging model can be used to predict seasonal and regional differences in feeding patterns for macaques (Agetsuma & Nakagawa, 1998).

Social Organization

Japanese macaques form multi-male multi-female groups that consist of at least two adult males and more than two adult females (Yamagiwa & Hill, 1998). Group sizes vary with weather-related resource availability. In sites where food is provisioned, group membership can reach several hundred individuals and one group was reported to reach 1,255 members (Thierry, 2011, p. 233; Yamagiwa & Hill, 1998, p. 259). In non-provisioned sites group size is significantly lower, rarely reaching above 100 members (Thierry, 2011). Groups can also be categorized as fission-fusion groups and the average size of undisturbed and unprovisioned groups can range between 50 to 70 individuals before splitting (Menard, 2004).

Environmental factors such as temperature, snowfall, and the quality of food influences the size that fission-fusion groups can reach. Groups that inhabit deciduous forests with heavy snowfall tend to be larger than groups in evergreen forests, subtropical forests, and areas with light snowfall, (Menard, 2004; Yamagiwa & Hill, 1998). It would be expected that the average group size will become smaller in response to the restricted access to food in regions with heavy snowfall, but the larger group sizes can be explained by having a larger range. Groups that live in regions with heavy snowfall with deciduous forests are spread apart over greater distances and groups that live in subtropical forests can forage in closer proximity to each other (Agetsuma & Nakagawa, 1998). The smaller groups in subtropical forests have a high population density while the larger groups spread over a greater distance.

Female Japanese macaques are philopatric, forming kin bonds, and the hierarchies of female-bonded groups tend to be linear and stable with a high degree of nepotism (Thierry, 2011; Yamagiwa & Hill, 1998). Rank among females is not correlated with physical strength and daughters inherit their mother's rank (Chapais, 1988). A daughter will outrank any member of the group her mother outranks (Chapais, 1988). The youngest daughter is usually higher ranked than her older sisters because the mother usually supports her (Thierry, 2011).

While females inherit rank from their mother, their rank also depends on support from other females (Chapais, 1988). Subordinates will challenge dominants if they are more physically imposing than the dominant (Chapais, 1988). This strategy is used mostly by younger conspecifics (Chapais, 1988). While matrilineal hierarchies tend to be stable, females may opportunistically attack a higher ranking individual if the latter has no support nearby. This suggests that the Japanese macaque has a social intelligence allows them to regulate behavior by taking into account the dominance of nearby animals (Call, 2004).

Non-kin coalitions rarely form between females due to the high degree of nepotism. As nepotism increases, stronger hierarchies are formed and the difference of rank between non-kin groups becomes greater (Thierry, 2011). The stable and linear hierarchy that forms due to the strong nepotism within Japanese macaque groups also means that the outcome of contests is unidirectional, and fights rarely escalate into biting (Chapais et al., 1991; Thierry, 2011).

Females can exert a high degree of choice in mating and there is little or no correlation between rank and reproductive success for males. Higher ranked males will attempt to interrupt mounting between lower ranked males and females, but females will rarely allow themselves to be mounted by the higher ranked male after interruption (Takahata, 1982). Rank among males is correlated with tenure within a group, and males joining new groups usually enter at a low rank (Berard, 1999). Males usually leave their natal group before sexual maturation, which prevents them from forming alliances between related kin (Thierry, 2011; Yamagiwa & Hill, 1998). Males also rarely form coalitions with non-kin, as they compete aggressively over females and sexual reproduction is a zero-sum game. Males rarely assist each other in conflicts unless there is a shared interest such as defending shared food or defending females in their group from foreign males (Majolo et al., 2005).

Japanese macaques are less likely to partake in reconciliation than other species of macaques (Thierry, 2011). After most fights, individuals involved in the conflict spend more time self-grooming and rarely attempt to reconcile with the other member involved in the fight (Daniel & Alves, 2015). Experimental studies have shown that macaques choose to associate with other bystanders instead of with those involved in the conflict (Daniel & Alves, 2015). Majolo et al. (2005) argue that consolation does not occur because individuals do not possess the cognitive ability for empathy that is required for consolation. While Japanese macaques may be aware of the social status of other animals, most research suggests this is not based on understanding psychological states (Call, 2004).

Summary

Japanese macaques are a behaviorally flexible species exploiting habitats that range from sea coasts to more temperate mountain ranges. This is partially enabled by morphological adaptations for colder climates like denser fur and larger body mass. They also demonstrate the ability to adjust group size in response to their environment. In instances where food is provisioned, they can form groups that number in the hundreds. In habitats without provisioned foods, researchers have found that Japanese macaques will form larger groups over large ranges in response to restricted access to food but will form small groups with smaller ranges in response to food abundance. They form groups that are characterized by highly despotic nepotistic matrilineal hierarchies with few non-kin coalitions. It is difficult to tell if Japanese macaques do not form non-kin alliances due to a lack of cognitive ability or empathy, or due to the increased competition created in larger groups. More field studies comparing affiliative behavior between provisioned and unprovisioned groups are needed to elucidate how environmental pressures influence the species' likelihood of forming non-kin affiliations.

The Behavior and Ecology of the Black-Handed Spider Monkey (*Ateles geoffroyi*)

Taxonomy and Morphology

The genus *Ateles* belongs to the family *Atelidae* and the sub-family *Ateline.* The genus is currently made up of 4 separate species. Earlier taxonomic models such as one proposed by Kellogg and Goldman in 1944 divided the genus into 4 species known as *Ateles geoffroyi, Ateles fusciceps, Ateles belzebuth,* and *Ateles paniscus* (Collins, 2008; Collins & Dubach, 2000). Species were demarcated by observable differences in pelage coloration observed among the different spider monkey populations throughout Central and South America (Collins, 2008). In Goldman and Kellogg's proposed taxonomy, *A. geoffroyi* had 16 subspecies that were distinguished by possessing dark black heads, black hands, and black wrists (Collins, 2008). Various subspecies were identified by the color of their undersides and hind limbs, which could range from brownish, silvery, or to a light golden hue (Collins, 2008).

The taxonomy based on coloration overlooked the overlap in pelage coloration between subspecies and ignored geographic barriers between species and subspecies (Collins, 2008; Collins & Dubach, 2000). It did not examine the gene flow between subspecies and species, and did not model how speciation could have occurred. In response, different models that look at chromosomal analysis and the measurements of cranial sizes to determine phylogenetic relationships are proposed (Collins, 2008; Morales-Jimenez, Cortes-Ortiz, & Di Fiore, 2015).

A newer model uses parsimony and neighbor-joining analysis to create a new taxonomic model (Collins & Dubach, 2000). This model suggests that there are four separate species within the genus *Ateles*: *A. belzebuth, A. paniscus, A. geoffroyi,* and *A. hybridus* (Collins, 2008). This model designates *Ateles fusciceps* as a subspecies of *A. geoffroyi.* This model proposes three clades within *A. geoffroyi* called the Northern clade, Southern clade, and a third clade that is currently unnamed (Collins, 2008). This new model has problems establishing subspecies among *A. geoffroyi,* and it is still uncertain if *A. fusciceps* should be considered a sub-species of *A. geoffroyi* (Morales-Jimenez, Cortes-Ortiz, & Di Fiore, 2015).

Another model challenges Collins' and Dubach's phylogeny model through the use of a more robust mtDNA analysis using 23 samples from seven different species of spider monkeys (Morales-Jimenez, Cortes-Ortiz, & Di Fiore, 2015). This newer mtDNA analysis suggests that there are at least 2 clades for the species *A. geoffroyi*: a southern clade composed of *A. g. panamensis*, and a northern clade composed of *A. g. yucatanesis* and *A. g. vellerosus* (Morales-Jimenez, Cortes-Ortiz, & Di Fiore, 2015). The analysis also suggests *A. g. fusciceps* should not be considered a sub-species of *A. geoffroyi* because the genetic distance is greater between *A. g. fusciceps* and *A. geoffroyi* than what is currently posited by the study by Collins and Dubach

(Morales-Jimenez, Cortes-Ortiz, & Di Fiore, 2015). It is argued that the presence of a hybrid zone does not mean that the two populations should be considered part of the same species (Morale-Jimenez, Disotell, & Di Fiore, 2015). This analysis also suggests the third clade should encompass the subspecies *A. g. azurensis* and *A. g. ornatus* (Morale-Jimenez, Disotell, & Di Fiore, 2015).

These new studies demonstrate the ineffectiveness of relying on pelage coloration for taxonomic classification of *A. geoffroyi*. Despite the disagreement of the placement of *A. g. fusciceps* as either a separate species or a subspecies of *A. geoffroyi,* there is agreement that there are at least three clades of subspecies.

Despite the inability to differentiate subspecies by pelage color, *A. geoffroyi* can be characterized by the shared traits of black wrists, black hands, and a black head. Males and females are not significantly sexually dimorphic in body size, with males weighing an average of 8.2 kg and females weighing an average of 7.4 kg (Ford & Davis, 1992). The skull is gracile with large orbits and a globular shape (Rosenberger et al., 2008). Although there is little sexual dimorphism in skull shape there appears to be a sex difference in growth rate. Females experience a rapid growth spurt in the cranial region during a developmental age designated as D4, defined by the presence of at least one canine reaching the occlusal plane, and then a slowing down of growth in the cranial region when all of their permanent dentition is in place (Corner & Richtsmeier, 1993). In contrast, males experience a slower growth rate during the D4 developmental age and will have a smaller crania compared to females during that developmental period.

The genus *Ateles* uses multiple means of locomotion such as brachiation and arboreal quadrupedalism (Fleagle, 1999a; Fontaine, 1990). The genus *Ateles* has developed some morphological adaptations to exploit its environment in the canopy. All members of this genus possess long and slender limbs, elongated prehensile tails, and elongated phalanges (Di Fiore et al., 2008; Fleagle, 1999a; Rosenberger et al., 2008). Most members have reduced thumbs and a shorter trunk due to a reduced lumbar (Fontaine, 1990). Some analysts argue that brachiation can explain the reduced lumbar, but this trait is also shared by the genus *Cebus,* which relies more on climbing than brachiation (Fontaine, 1990). Other analysts point to a suite of abilities requiring the bending of the body and the use of prehensile tails as a better explanation for a reduced trunk than the ability to brachiate (Fontaine, 1990).

Ecology and Diet

The genus *Ateles* is widely distributed across Central and South America, and *A. geoffroyi* is found in Mexico, Costa Rica, and Columbia (Figure 3) (Di Fiore et al., 2011; Zaldivar et al., 2004). *A. geoffroyi* inhabits tropical, semi-evergreen forests, deciduous forests, and semi-deciduous forests (Chapman et al., 1995). These regions experience a dry season from January through May and a rainy season from June through December (Chaves, Stone, & Arroyo-Rodriguez, 2011). The two seasons determine which resources are exploited because fruit can become

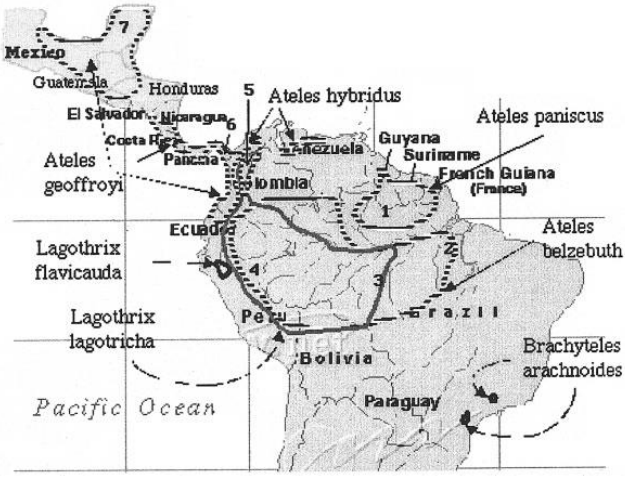


Figure 3: Map of the ranges of the family *Atelines*. *A geoffroyi* range extends from Mexico to the northwestern coast of South America (A. C. Collins, 2004).

scarce during the dry season (Chaves, Stone, & Arroyo-Rodriguez, 2011). *A. geoffroyi* displays flexibility in terms of diet, activity budget, and social structure in response to challenges presented by climatic variability.

Spider monkeys are ripe fruit specialists, as much of their diet consists of either mature or ripe fruit (Di Fiore et al., 2008). They have a short gut passage to digest fruits and have difficulty digesting foliage (Schaffner et al., 2012). *A. geoffroyi* has been observed to exploit foliage as a fallback food in times of fruit scarcity. Two investigations compare the diet of a population of *A. g. yucantensis* before and after hurricane Emily. (Schaffner et al., 2012). The first investigation finds that the monkeys spent more time eating fruits eight weeks after the hurricane, but this was only because the hurricane caused most of the primary fruit-bearing branches to fall to the ground (Schaffner et al., 2012). A follow up study finds that the spider monkeys spent less time eating fruit and more time eating foliage during the dry seasons after Hurricane Emily than they did during the dry season before the hurricane (Schaffner et al., 2012). Spider monkeys can eat foilage in the absense of fruit, but they can not subsist solely on foilage for long periods of time without negative side-effects, including weight loss and dermititis (Schaffner et al., 2012). Additional studies suggest wood is consumed as a source of sodium and calcium as these nutrients may not be available in the fruits that they eat (Chaves, Stone, Angeles-Campos, & Arroyo-Rodriquez, 2011).

This species' activity and range are also influenced by seasonal changes and forest fragmentation. During the dry season *A. geoffroyi* reduces energy consumption and increases resting time in response to the harsher conditions (Chaves, Stone, & Arroyo-Rodriguez, 2011). In a fifteen-month study at Lacandona Rain Forest, researchers observe six independent *A.*

geoffroyi communities: three located in continuous forests and three located in fragmented forests (Chaves, Stone, & Arroyo-Rodriguez, 2011). The authors hypothesize that resting times will increase during the dry season in fragmented forests, but the research finds there is no difference in dry-season resting times for both continuous-forest and fragmented-forest groups. Instead, the study suggests that during the dry season groups in fragmented forests spent more time feeding, while groups in continuous forests spent more time travelling.

Social Behavior

A. geoffroyi groups can vary in size. A study that consists of 18 spider monkey groups from 5 different species, and four of these 18 groups consist of members from the species *A. geoffroyi* finds a mean group size of 34.5 individuals among the *A. geoffroyi* groups. However, group size varies widely, from as high as 75 members to as low as 20 members (Shimooka et al., 2008). The wide range of members is because *A. geoffroyi* is capable of adjusting their group size in response to environmental pressures, such as weather phenomena and seasonal patterns, to their habitat (Aureli & Schaffner, 2008).

Spider monkeys live in fission-fusion groups where individuals merge to form larger groups to avoid predation, but competition for food increases as group size increases (Terborgh & Janson, 1986). Groups must balance the selective pressure of predation against resource competition. Their large body and habitat in the upper canopy allows this species to avoid predation so they can split into smaller groups to reduce competition (Aureli & Schaffner, 2008; Schaffner et al., 2012; Chapman et al., 1995). These communities also adjust their group size in response to the different seasons by adjusting their activity and diet (Schaffner et al., 2012).

Most communities are segregated by sex, and the philopatric males form strong affiliative male-male bonds, while females disperse from their natal group and form cooperative communities with overlapping ranges (Di Fiore et al., 2011; Ramos-Fernandez et al., 2009; Fedigan & Baxter, 1984). Females maintain affiliations with other females similar in age; however, females also direct their affiliative behavior with other conspecifics regardless of age or sex (Fedigan & Baxter, 1984). The patchy distribution of nutritious food allows females to disperse over a large range. The environment of the canopy allows for females to cooperate by monitoring of females over the top of the canopy. The dispersal and monitoring prevents males from effectively employing mate guarding as a tactic for sexual reproductive success as females are not clumped together and have the relatively same body size (Fedigan & Baxter, 1984; Wrangham, 1980). Males, in response, form cooperative groups to control a range overlapping with several females instead of competing with each other. The low degree of sexual dimorphism due to lack of competition between males and the patchy distribution may be the reason for the sexual segregation among this species.

In the past, it was generally thought that females were solitary and form weaker bonds with other females or males. However, a study by Ramos-Fernandez et al. (2009) questions this position, finding that associations between females are stronger than associations between males. Four clusters of association are identified in this analysis: immigrating females, resident females, adult males, and emigrating females. The study finds that females were not selective with whom they associated with and argues that females form the core of the social group because female bonds are more stable than male bonds with associations lasting over long periods of time. Females aggregate as the core, but males do form close relationships with other males at the periphery of the group. The only exception is that recent female immigrants are also on the periphery and maintain close bonds with only a few members rather than aggregate among the core of the group. The authors concludes that the relationships in female-female bonded groups may be stronger than what previous researchers have thought. While their results derive from a single group, the eight year duration of the study may mean patterns were observed that could not be detected in shorter term studies.

Summary

The black-handed spider monkey is a behaviorally flexible species that forms fission-fusion groups. The degree of flexibility of their fission-fusion groups allows them to adapt to forest fragmentation and changes in their environment. The high degree of flexibility can be attributed to being large-bodied frugivores that do not face the strong selective pressures of predation. Males can form stronger bonds because males remain in their natal group while females disperse. Recent research suggests that bonds between females may be stronger than researchers have previously believed.

Chapter 3: Environment and Hierarchy

Most non-human primates are social animals that form complex social groups and will form hierarchies within those social groups. The purpose of this chapter is to explain how the environment influences linearity within social groups and hierarchies through the spatial-temporal distributions of resources and risks (Kappeler & Schaik, 2002). The way members distribute themselves according to these risks influences the type of competition that members will face within their environment. Hierarchies are a response to that competition.

This chapter will first explore how the spatial distribution of food and predation risk influence the size and organization of primate groups. I will then explain what hierarchies are and discuss their characterization on three dimensions: nepotism, tolerance, and linearity. Finally, I will explain how competition helps shape the linearity within a hierarchy and provide examples of despotic and egalitarian hierarchies.

Group Size and Organization

How females organize themselves within an environment is one of the basic influences on group size and organization. It is assumed that females distribute themselves according to the spatial-temporal distribution of food and risks encountered within an environment, while males distribute themselves according to the spatial-temporal distribution of females (Fuentes, 2011; Kappeler & Schaik, 2002). Males and females organize themselves per different criteria because each sex faces different selective pressures for reproductive success. Access to females limits reproductive success, and access to food limits female reproductive success due to the energy and time of gestation (Strier, 2007). The distribution of food and the risk of predation influences the social relationships within a group in three ways: female gregariousness, competitive regime, and social relationships (Fuentes, 2011; Sterck et al., 1997). Female gregariousness reduces the risk of predation by having multiple members watch for predators, through a herd dilution effect that reduces the chance of any individual to be attacked by a predator, and by communal defense (Fuentes, 2011; Kappeler & Schaik, 2002; Sterck et al., 1997).

The risk of predation interacts with the spatial-temporal distribution of food and influences group size, which affects the type of competition individuals face (Sterck et al., 1997). Groups that do not successfully adjust size to balance food availability and predation risks may die out. Fission-fusion groups like the black-handed spider monkey (*Ateles geoffroyi)* and the Japanese macaque (*Macaca fuscata*) can adjust the size of their group in response to the availability of food (Menard, 2004; Schaffner et al., 2012; Sterck et al., 1997). Black-handed spider monkeys are known to change group size in response to environmental seasonality and Japanese macaques flexibly adjust group size in accordance with the resources available (Schaffner et al., 2012, Thierry, 2011; Yamagiwa & Hill, 1998).

The temporal-spatial distribution of food determines whether groups will face either scramble competition or contest competition. Scramble competition is a competition against time and space to gather food that is not clumped together (Fuentes, 2011). Thus, members within a group share food equally (Fuentes, 2011). Contest competition is a competition between individuals over food that is clumped together. In response, members in a group are able defend that source of food from other conspecifics (Fuentes, 2011; Sterck et al., 1997). Food can be monopolized during contest competition, but not during scramble competition.

The time it takes to eat the food is an important variable determining whether a food item can be monopolizable. Foods like fruit and meats require a long depletion time so they can be usurped and easily monopolized (Isbell & Pruetz, 1998). Foods like foliage have a quick depletion time where an individual can quickly extract or eat a food item and so cannot be usurped (Isbell & Pruetz, 1998).

Social structure, social relationships, and hierarchies form in response to these types of competition regimes. Large female-bonded groups form in response to contest competition, and smaller groups form in response to scramble competition (Fuentes, 2011; Sterck et al., 1997). The more intense competition in contest competition regimes increases the need for allies to help individuals avoid being supplanted by other individuals or to supplant others to gain access to a preferred food source (Wrangham, 1980). Female groups that form in response to scramble competition are usually have weak bonds (Fuentes, 2011; Sterck et al., 1997). It is an adaptive strategy for females to spread out in response to scramble competition to avoid inflicting reproductive costs on kin (Wrangham, 1980).

Hierarchies and Its Dimensions

A hierarchy is a relatively stable ranking that is defined as a dominance order established through agonistic encounters, is acknowledged by the animals within a social group, and determines priority of access to reproductive opportunities or food (Alberts et al., 2003; de Waal, 2013; Maestripieri, 2012; Manson, 2011; Strier, 2007). Non-human primates show an awareness of their status within a group through the use of signals like the fear-grin, which subordinates direct towards dominants to establish that they are not a threat to the more dominant individual (de Waal, 1989a). The hierarchies observed in primate groups can be understood through three dimensions: nepotism, tolerance, and linearity (Sterck et al., 1997).

Nepotism is how often members receive coalitional support or help from relatives (Jaeggi et al., 2010). Strong female-bonded groups where female conspecifics do not leave their natal group often exhibit high levels of nepotistic support (Fuentes, 2011; Sterck et al., 1997; Strier, 2007). The type of competition determines whether males or females will disperse from their natal group: females disperse in scramble competition, and males during contest competition (Fuentes, 2011; Strier, 2007). In the absence of a strong female hierarchy males form male-bonded groups and will receive a mixture of support from both non-kin and matrilineal kin (Boehm, 1999; Stumpf, 2011).

Tolerance measures the frequency and severity of aggression within a group (Sterck et al., 1997). The more tolerant a social group, the lower frequency and severity of aggression between members. In more tolerant groups aggression is not directed unilaterally from dominants to subordinates, and subordinates may direct threats to dominants (Sterck et al., 1997). A group that is more tolerant could have a linear hierarchy where a dominant tries to exclude subordinates from food or mating, but often the dominant will accept the presence of the subordinate (de Waal & Luttrell, 1989). Tolerance explains situations where a dominance hierarchy does not perfectly predict the priority of access to food or mating (de Waal, 1989a).

Primate social groups exist along a continuum running from non-linear to linear hierarchal structures. Linearity is a measurement of how often dominants unilaterally win dyadic conflicts (Sterck et al., 1997). In linear despotic hierarchies, dominants have a higher probability of exclusively winning conflicts. As the imbalance between subordinates and dominants becomes more even, the dominance relationships are less clear and the hierarchy becomes more egalitarian and non-linear (Maestripieri, 2012; Sterck et al., 1997). A linear hierarchy can be understood in terms of transitive logic: if A>B and B>C, then A>C. In a linear hierarchy, C will always be subordinate to both A and B, and B will only be subordinate to A. Non-linear hierarchies are non-transitive: A>B and B>C, but C may be dominant over A (Maestripieri, 2012). A hierarchy is more despotic if there are more linear dominance relationships, and a hierarchy is egalitarian if dominance relationships are more non-linear (Sterck et al., 1997). Linearity of dominance relationships determines the steepness of a hierarchy. The ability of dominants to consistently win antagonistic dyadic encounters against subordinates or to consistently supplant subordinates is a measurement of hierarchical steepness (Strier, 2007).

Members in a group use violence or the threat of violence to enforce hierachies, but despotic groups do not necessarily have more violent encounters than egalitarian groups. The difference between a despotic and an egalitarian group is not how often members fight each other but how often dominant members supplant subordinate members. In more egalitarian groups (e.g., patas monkeys) dominants do not always win conflicts. Chimpanzees (*Pan troglodytes)* also form egalitarian multi-male groups but exhibit high frequencies of violent interactions, especially when males are attempting to move up the hierarchy (Boehm, 1999). In contrast, the more despotic matrilineal hierarchies of Bonobos (*Pan paniscus)* exhibit lower levels of violence (Jaeggi et al., 2010). Instead, males rely on support from related females, such as their mothers, to climb the male social ladder (de Waal, 2013).

Influences of Ecology on Linearity

The type of competition between members influences the steepness of a hierarchy. Stronger female linear hierarchies form in response to environments that promote contest competition and create strong within-group competition (Sterck et al., 1997). A long-term study comparing vervet monkeys (*Cercopithecus aethiops*) and patas monkeys (*Erythrocedus patas)* at Segera Ranch in north-central Kenya illustrates this dynamic. Both vervets and patas monkeys exhibit female-bonded groups, but patas monkeys feed on leaves while vervets feed on fruits (Isbell & Pruetz, 1998). Among the vervets there is a 0% rate of reversals in aggressive interactions while the patas monkeys have an 18% rate of reversals (Isbell & Pruetz, 1998). The difference of distribution of food that each species' prefer leads to differences in hierarchy. Vervets have to compete for foods such as fruit while the patas monkeys are engaging in a scramble competition for leaves. The study also demonstrates that the hierarchy of vervets is steeper than the patas monkey hierarchy.

A follow-up study reinforces this conclusion noting that vervets exploite food from both *Acacia drepanolobium* trees and *Acacia xanthophloea* trees, while patas monkeys get their food mostly from *A. drepanolobium* trees (Pruetz & Isbell, 2000). The social groups exhibit weaker linear hierarchies, but there is a correlation of the linear hierarchies with the random distribution of *A. drepanolobium* trees. This follow-up study finds that overall, vervets have more linear hierarchies and most vervet agonistic interactions occur in *A. xanthophloea* trees correlating with a clumped distribution of trees.

When analyzing characteristics of hierarchies males and females must be treated separately because reproductive selective pressures cause them to organize themselves differently. For example, gorillas can form either a single-male/multi-female group or a multi-male/multi-female group (Robbins, 2007). In either multi-male or single-male groups, males typically form a steep despotic hierarchy where a lone silverback gorilla is always dominant over all blackback gorillas and all female gorillas (Robbins, 2007). These groups are despotic to the point where males are able to subject sexually active females are often subjected to harassment and the silverback gorilla is able to influence the direction the group will travel (Boehm, 1999; Robbins, 2007). In contrast, the females in single-male/multi-female groups tend to form non-bonded female groups where related females will disperse after a certain age (Robbins, 2007). As a result, female relationships among gorillas tend to be egalitarian with a loose hierarchy (Robbins, 2007).

Summary

The spatial-temporal distribution of food and predation influences the linearity, nepotism, and tolerance that characterize primate social hierarchies. As males and females face different limiting factors for reproductive success, environmental pressures influence the social relationships for each sex differently. Females distribute themselves according to the risks of predation and food, and males distribute themselves accordingly to how females are organized. Males will disperse and form loose bonds and females will form strong bonds within matrilineal hierarchies with a strong degree of female nepotism. Males will form stronger bonds between themselves and females will disperse in the absence of a strong matrilineal hierarchy.

The distribution of food creates the type of feeding competition within a group, which determines how linear the hierarchy will be. Groups facing contest competition will exhibit stronger within-group competition and females will stay in their natal groups. Females in such groups may form strong alliances to protect access to food. Despotic hierarchies can be created because of the competition between members. In contrast, in groups facing scramble competition females will disperse to prevent feeding competition. Scramble competition will typically lead to more egalitarian hierarchies as females form looser bonds and often leave their natal group. The distribution of food and the type of competition is important in deciding the expression of a group's hierarchy, but there are times when a species may use another adaptive strategy to diffuse within-group competition. Egalitarian species such as the black-handed spider monkey may adjust group size through fission or fusion in response to the resources available in the environment. The next chapter will discuss how hierarchies shape cooperation in social groups. It will also discuss how hierarchies shape cooperation for both the black-handed spider monkey and the Japanese macaque.

Chapter 4: Cooperation within Hierarchies

Many primate species exhibit cooperative behavior such as the sharing of food, coming to the aid of allies, and grooming [e.g., chacma baboons (*Papio ursinus*), rhesus macaques (*Macaca mulatta*), chimpanzees (*Pan troglodytes)* and bonobos (*Pan paniscus)*]. The purpose of this chapter is to explain how the steepness of hierarchies influence the extent and nature of cooperation between group members. As noted earlier, hierarchies range from despotic to egalitarian. Typically, grooming goes from subordinates to dominants in more despotic hierarchies. Recent studies demonstrate that the introduction of resources that can be obtained only through joint effort can lead to cooperation. In addition, other studies have found that tolerance for other members can result in the priority of access that is typical of steep hierarchies to be ignored. The literature review of this thesis will conclude by providing examples of how hierarchy influences cooperative behavior among the Japanese macaque (*Macaca fuscata)* and the black-handed spider monkey (*Ateles geoffroyi*), paying some attention to how captivity may modify patterns found in the wild.

Cooperation and Social Hierarchies

Hierarchy influences how primates cooperate with conspecifics. Studies suggest that there is a relationship between steepness and the sharing of food and grooming, such that subordinates will direct grooming and food unilaterally towards dominants (Jaeggi et al., 2010). However, additional studies demonstrate that the introduction of shared resources also leads to further defined hierarchies among already despotic species, despite the need for cooperation. Other studies demonstrate how tolerance influences cooperation between members despite the presence of a steep hierarchy. This demonstrates that linearity, nepotism, and tolerances all influence how members will cooperate within a hierarchy.

It was originally argued that cooperative behavior would not evolve in more despotic primate species because aid from other individuals would disrupt the stability of dominance ranks (Triver, 1971). However, co-feeding and other forms of cooperation is observed among despotic species such as chacma baboons (*Papio ursinus)* and rhesus macaques (*Macaca mulatta*) (King et al., 2011). Dominant chacma baboons co-feed and tolerate non-kin subordinates who have previously groomed the dominant (King et al., 2011). Rhesus macaque male and female consort pairs will co-feed at feeding spots that contain resources they can monopolize, but incoming males will often displace females that do not have partners from monopolizable feeding spots (Dubuc et al., 2012). Hierarchy rank and social relationships between pairs become important factors in determining who these species may cooperate with.

Chimpanzees are typically considered more egalitarian and bonobos are normally considered more despotic in comparison. A comparison of a captive chimpanzee group at the Abenteuerland Walter Zoo in Switzerland and a captive bonobo group at Dierenpark in Belgium found that the more egalitarian chimpanzee group was more tolerant of food transfers and had less forced transfers in comparison to more despotic bonobos (Jaeggi et al., 2010). The study suggested that hierarchy was important in determining the rates of reciprocity within a non-human primate group. The steeper the hierarchy the more likely the exchanges are to be unidirectional towards dominant members because the cost of defending a monopolizable food item is higher than in a steep hierarchy (Jaeggi et al., 2010). Additional studies observing other bonobo groups present similar results. The studies find that there is a significant correlation between grooming and support received among a bonobo group at the Wild Animal Park Planckendael located in Belgium (Vervaecke et al., 2000). The higher ranked individuals are groomed more often by lower ranked individuals, and higher ranked individuals groom the lower ranked individuals less frequently (Vervaecke et al., 2000).

Conversely, the introduction of shareable resources and the need for cooperation may also influence the dominance hierarchies within a non-human primate group. A group of vervet monkeys at the Mpumalanga province in South Africa segregate themselves into different groups of similar rank in an experiment that requires cooperation to gain access for food from feeders (Pansini, 2011). To gain food from the feeders, the wild vervets were trained to push a button on the feeder, which required individuals to cooperate to successfully get food from the feeder. The introduction of the feeders caused higher rates of antagonism and members responded by only approaching the feeders if their preferred partners were present, while avoiding other group members. Cooperation is induced by the distribution of resources, and dominants will only cooperate with other dominants and subordinates will only cooperate with other subordinates. The increase of antagonism and segregation according to dominance rank suggests that the inclusion of shareable resources increases tolerance among individuals similar in rank, but decreases tolerance among dominants towards subordinates.

A study of rhesus macaques also demonstrates how hierarchy and tolerance can influence the way group members cooperate. The macaques were deprived of water for three hours, after which a large basin allowing more than one monkey to drink at the same time was brought in to their enclosure (de Waal, 1989b). Most individuals cooperated and drank together, although subordinates did wait for a turn while dominants drank first. Tolerance was not uniformly distributed throughout the hierarchy: there were two classes comprised of high ranked individuals and low ranked individuals and individuals were tolerant only of others within their own class, but members from different classes would exclude the other.

Cooperation does occur within despotic hierarchies. Studies comparing chimpanzees and bonobos suggest that stricter hierarchies inhibit the transfer of food and affiliative behavior, but a study of vervet monkeys suggests that the introduction of shareable resources and affiliative behaviors can also serve to reinforce dominance rank. The rhesus macaques also segregate into groups influenced by hierarchal rank with the introduction of shareable resources. These studies suggest that the introduction of resources will cause members to naturally form hierarchies so members of similar rank will cooperate with each other to maintain access to those resources. However, too steep of a hierarchy can eventually inhibit cooperation between members that are not kin.

Cooperation and Hierarchy among the Black-Hand Spider Monkey and the Japanese Macaque

The linearity of dominance hierarchy influences cooperation between individuals among both Japanese macaques and black-handed spider monkeys. As previously discussed, Japanese macaques form strict despotic matriline hierarchies where related females form strong bonds (Thierry, 2011; Yamagiwa & Hill, 1998). Male macaques also form multi-male groups but these exhibit weaker bonds than female networks because males are often unrelated (Berard, 1999). In contrast, the rarity of agonistic behavior among black-handed spider monkeys often makes it difficult to determine if there is a dominance ranking among conspecifics (Fedigan & Baxter, 1984). Male spider monkeys are more likely to form cohesive groups and display affiliative behavior while females are less likely to display affiliative behavior (Fedigan & Baxter, 1984). Both primate species display different patterns of cooperation and affiliation that are influenced by the linearity of their social groups.

Male Japanese macaques are less likely to display cooperative behavior than females and rarely, if ever, engage in cooperative acts (Majolo et al., 2005). There are several factors that account for the lack of cooperative behavior between males. Food often cannot be shared and mating is a zero-sum game with a high degree of female choice (Majolo et al., 2005; Takahata, 1982). Further, males within Japanese macaque social groups are often unrelated, so there is little reason for males to form coalitions or build relationships through cooperative behavior (Majolo et al., 2005). The absence of kinship bonds among males is a strong factor as to why males rarely cooperate. In contrast, females form stable and linear hierarchies of related kin. Non-kin coalitions are rare among females but are not entirely absent.

A study by Chapais et al. (1991) observes fifteen individuals from three matrilines in the Arashiyama troop transplanted to Texas. Members from Matriline A are dominant over members in matriline B and C, and members from matriline B are dominant over members in matriline C. The study finds that 73% of the time, members in matriline A prefers to provide support to members of matriline B over members of matriline C, while 85% of the time, members of matriline B prefers to provide support to members of matriline A over members of matriline C. Members of matriline C rarely provides coalition support to members from either matriline A or B. It is possible that there is a greater incentive for members of high-ranking and mid-ranking matrilines to form coalitions against members of lower ranked matrilines so females do not not have to expend time and energy to constantly protect their rank (Chapais et al., 1991). Within despotic hierarchies, the threat of violence protects the rank of higher members as dominant direct threats and aggression unilaterally to subordinates (Chapais et al., 2011). High ranking members are more likely to receive support or experience cooperation with members from lower ranks.

Cooperation among black-handed spider monkeys is influenced by the fact that females disperse from their natal group while males form strong kin-bonds (Foire et al., 2011). As a result, males form cohesive groups (Fedigan & Baxter, 1984). In contrast, females do not necessarily form the same type of bonds that males form, and at first glace females appear to be solitary and submissive. However, it is possible that due to dispersal females actually form cooperative communities with overlapping ranges in the canopy of their environment.

A study at Tikal National Park observed a group of spider monkeys for 550 hours; the population ranged from 27 to 45 animals per square kilometer with a total population size of 225 animals (Fedigan & Baxter, 1984). Males exhibited higher frequencies of aggression and affinitive contact, (e.g., behaviors such as embracing), than females. Sometimes small sub-groups of two or three males would attack females, but females would rarely reciprocate the aggression. Fedigan's and Baxter's research suggests that males are more sociable and form stronger bonds than females. However, females gave more vocalizations during foraging even though they were observed to use affinitive contact less often than males.

The study concludes that females disperese as a means to form cooperative communities and to avoid male domination over a large range. Additional research using network analysis supports this claim finding that females formed the core of the social group while males were often on the periphery of the group (Ramos-Fernandez et al., 2009). In addition, another study using vocalization playback experiments finds that monkeys are more likely to approach the speakers that are used to playback recorded vocalizations if the recording was of a close associate (Ramos-Fernandez, 2004). The study itself does not indicate whether one sex or another were more likely to approach if the recording was of a close associate; however, an additional study may find a difference between how often males and females approach recorded playbacks. If females really do form cooperative networks, it is possible that while females do not use affinitive contact to maintain relationships, they cooperate using vocalizations. Such an adaptation would be more effective for a species that breaks into smaller sub-groups while dispersed over large ranges.

Summary

Among the despotic Japanese macaques strong matriline hierarchies are formed among females while males are loosely connected. Despite the assistance that female Japanese macaques receive from related sisters, we find that higher ranked members will often form coalitions with lower ranked members to maintain their rank. Japanese macaques will direct aggression unilaterally down the rank system. Higher ranked members are more likely to receive aid from lower ranked members. In contrast, spider monkeys have a much more egalitarian social structure where it is difficult to determine social rank. Females appear to form loose bonds and males form cohesive bonds to harass females. At first glance, females may not appear to form cohesive bonds, but research studying associations suggest that females form the central core of the social group and may use vocalizations to maintain relationships with each other.

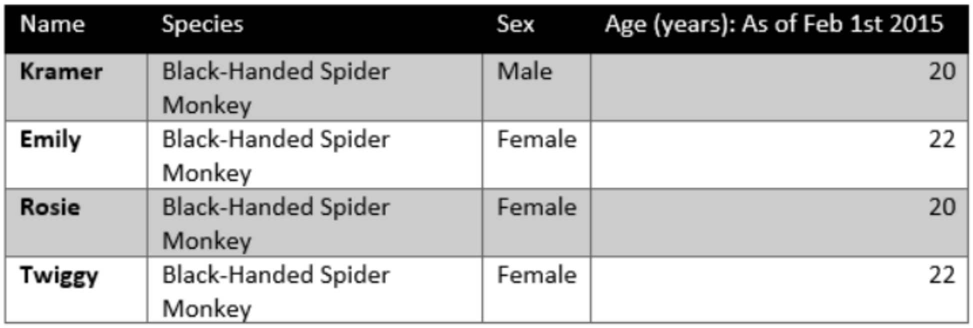
Chapter 5: Methods

The starting point for my research is the general expectation that there is a negative correlation between the steepness of a hierarchy and the frequency of cooperation: more despotic hierarchies are predicted to exhibit less cooperation than egalitarian ones. I tested this idea using two species that display different degrees of hierarchical steepness: egalitarian black-handed spider monkeys and despotic Japanese macaques.

The research on the spider monkey group was conducted at the Racine Zoo, located in Racine, WI. The research on the Japanese macaques was conducted at the Milwaukee County Zoo in Milwaukee, WI. Both zoos are open year-round and offer both outdoor and indoor enclosures for many of the primate species on exhibit. Data from the Racine Zoo were collected primarily between the hours of 10 am and 4 pm on weekends from February 2015 to May 2015. Data from the Milwaukee County Zoo were collected during the same hours on weekends from June 2015 to August 2015. Forty hours were spent observing the spider monkey group and 68.57 hours were spent observing the Japanese macaques.

Housing and Diet

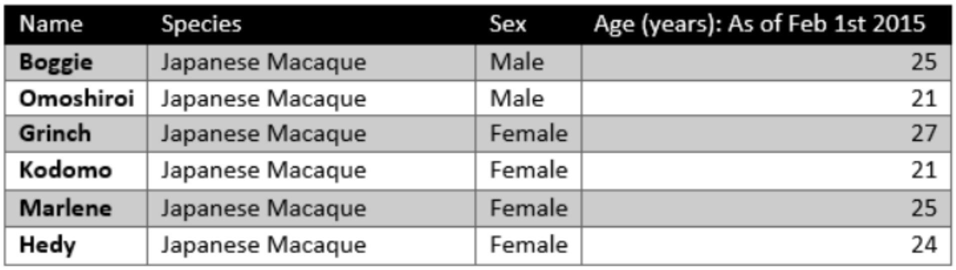
The spider monkey group (Table 1) at the Racine Zoo is composed of three females and one male (mean age: 21 years, range: 20-22). The group members' names are Emily, Kramer, Rosie, and Twiggy. Emily and Kramer are brother and sister. Kramer is completely blind and Emily is partially blind. Emily is the oldest in the group. The spider monkeys were housed in an indoor enclosure during the beginning of the study, but with warmer weather in late April the group was moved into a large outdoor enclosure. The indoor enclosure was a rectangular room with fake branches with swings attached, and the outdoor enclosure was an open space with a tree in the center. The troop had the freedom to move from the outdoor enclosure to the indoor enclosure during the warmer months of the year. Their diet consists of sweet potatoes, broccoli, celery, and assorted greens like kale and cabbage. The food was given to them in enrichment containers that required them to either open the container, reach inside the container, or even shake out food from the container. These enrichment containers were brought out daily, and there was at least one container for each monkey. The spider monkeys were also hand fed fruit and biscuits by keepers throughout the day.



Name	Species	Sex	Age (years): As of Feb 1st 2015
Kramer	Black-Handed Spider Monkey	Male	20
Emily	Black-Handed Spider Monkey	Female	22
Rosie	Black-Handed Spider Monkey	Female	20
Twiggy	Black-Handed Spider Monkey	Female	22

Table 1: Names, ages, and sex of Black-handed spider monkeys in the study.

The group of Japanese macaques (Table 2) at the Milwaukee Zoo consisted of four females and two males (mean age: 23.83 years, range: 21-25). The Milwaukee Zoo normally has a larger colony, but there were only six individuals in the colony at the time. The oldest is Marlene who is a sibling of Hedy and Omoshiroi. Boggie, Grinch and Kodomo may be related but their paternity is unclear. Like the group of spider monkeys, all individuals are adults. In warmer weather the macaques have free range access to both an indoor and outdoor enclosure. The outdoor enclosure is a large island surrounded by a moat. The island has a miniature mountain with various plateaus with enough room for members to lie down. In addition, the mountain has several entrances to a hollowed-out cave with enough room inside to house all six members. Members are hand-fed while indoors and out of the public view. Keepers also spread seeds throughout the island for foraging. The island also has different enrichment containers that can be used to store food. To avoid conflicts the keepers did not use these containers. All data was collected while the animals were in the outdoor enclosure.



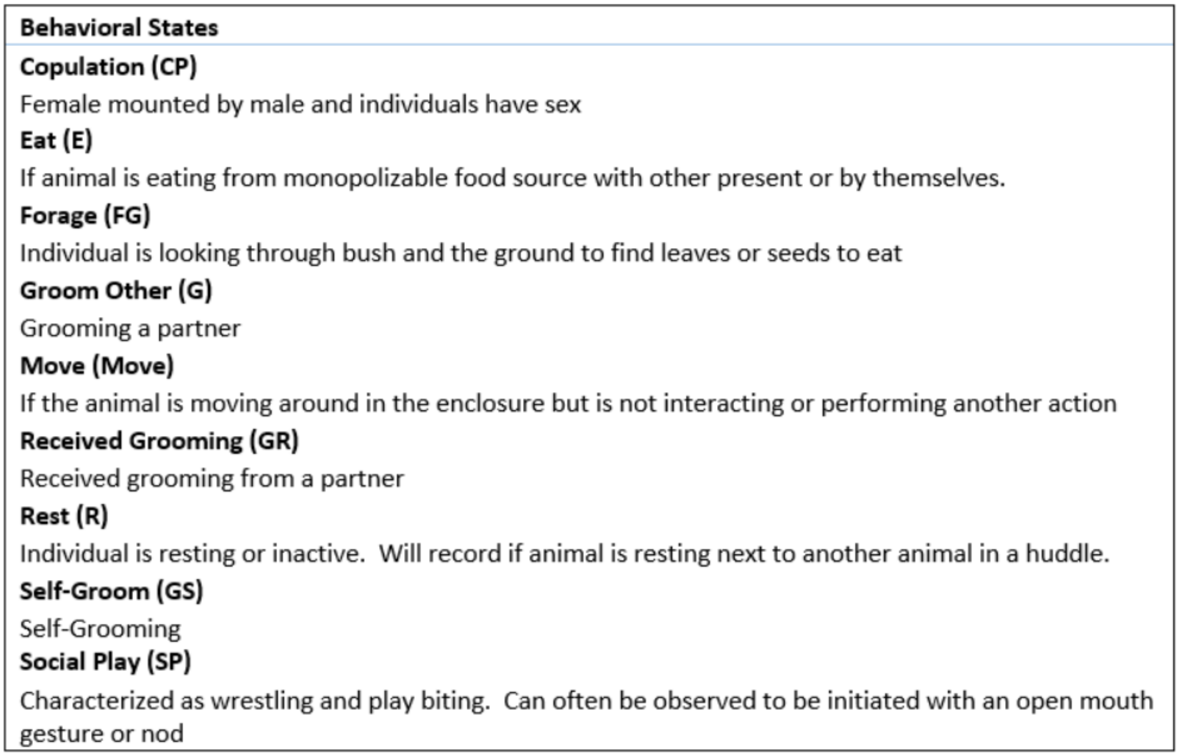
Name	Species	Sex	Age (years): As of Feb 1st 2015
Boggie	Japanese Macaque	Male	25
Omoshiroi	Japanese Macaque	Male	21
Grinch	Japanese Macaque	Female	27
Kodomo	Japanese Macaque	Female	21
Marlene	Japanese Macaque	Female	25
Hedy	Japanese Macaque	Female	24

Table 2: Names, ages, and sex of Japanese macaques in the study.

Data collection

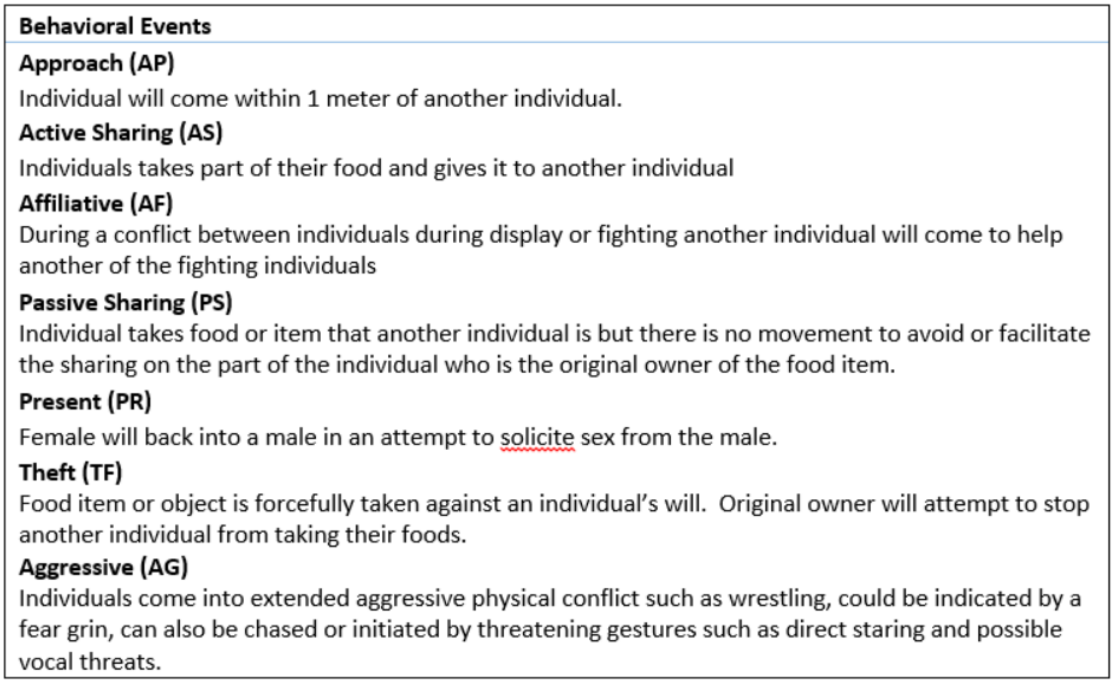
Data collection for both groups occurred while the animals were on display during open hours. Data were collected using focal animal sampling and the focal animal was observed for twelve-minute durations with a three-minute break between observations. If the focal animal was out of view for longer than two consecutive minutes the data were discarded. Agonistic behaviors and spatial association and displacement were recorded to determine the hierarchy for each group. The study also kept track of other behaviors (Table 3) such as grooming, social play, copulation, resting, eating, and food extraction from enrichment containers.

The study also recorded behavioral events (Table 4) such as the exchange of food in the form of passive sharing, theft, and active sharing. Theft was defined as an individual forcefully taking another individual's food (Boesch & Boesch, 1989). Passive sharing was defined as an individual taking an item from another without resistance, and active sharing was defined as the donor actively giving a portion of their food to another (Boesch & Boesch, 1989). Aggression was defined by behaviors such as yawns, biting, and fighting. Affiliative behaviors, such as coalitions coming to the defense of another individual, were recorded and the solicitation of sex from one individual to another was also recorded.



Behavioral States
Copulation (CP)
Female mounted by male and individuals have sex
Eat (E)
If animal is eating from monopolizable food source with other present or by themselves.
Forage (FG)
Individual is looking through bush and the ground to find leaves or seeds to eat
Groom Other (G)
Grooming a partner
Move (Move)
If the animal is moving around in the enclosure but is not interacting or performing another action
Received Grooming (GR)
Received grooming from a partner
Rest (R)
Individual is resting or inactive. Will record if animal is resting next to another animal in a huddle.
Self-Groom (GS)
Self-Grooming
Social Play (SP)
Characterized as wrestling and play biting. Can often be observed to be initiated with an open mouth gesture or nod

Table 3: List of behavioral states and definitions observed



Behavioral Events
Approach (AP) Individual will come within 1 meter of another individual.
Active Sharing (AS) Individuals takes part of their food and gives it to another individual
Affiliative (AF) During a conflict between individuals during display or fighting another individual will come to help another of the fighting individuals
Passive Sharing (PS) Individual takes food or item that another individual is but there is no movement to avoid or facilitate the sharing on the part of the individual who is the original owner of the food item.
Present (PR) Female will back into a male in an attempt to solicite sex from the male.
Theft (TF) Food item or object is forcefully taken against an individual's will. Original owner will attempt to stop another individual from taking their foods.
Aggressive (AG) Individuals come into extended aggressive physical conflict such as wrestling, could be indicated by a fear grin, can also be chased or initiated by threatening gestures such as direct staring and possible vocal threats.

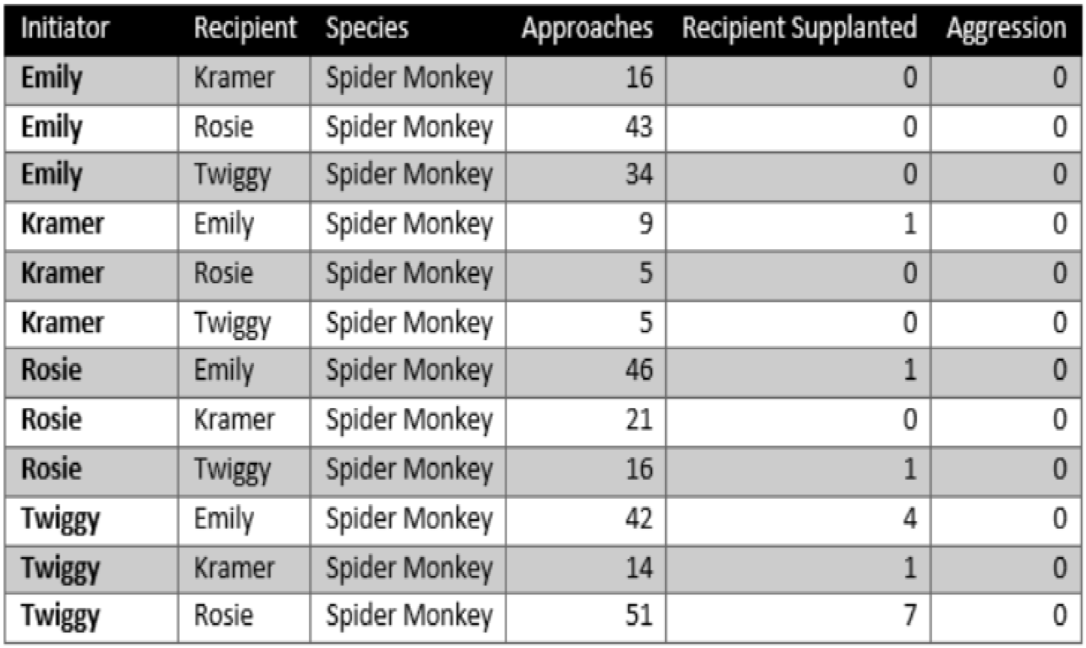
Table 4: List and definitions of observed behavioral events recorded.

Statistical Methods

Statistical work was performed using R version 3.2.2. This investigation used the David's score function within the EloRating package in R- to calculate each member's rank and to construct the hierarchies for each primate group. David's score was used because of the small size of the groups and the limited number of interactions in the data set. David's score calculates the dominance rank for individuals in a group based on the outcomes of dyadic interactions with other members (Gammell et al., 2002). Other dominance ranking methods, such as Clutton-Brock's system of hierarchy, are affected by minor deviations for small groups and these deviations will have a greater impact on a member's rank. David's score treats an individual's rank as independent of the interactions of other individuals and minor deviations do not have as great of an impact on the member's rank (Gammell et al., 2002). David's score weights defeating a higher ranked member more strongly than defeating a lower-ranked member (de Vries et al., 2006).

Two hierarchies were constructed for each group in the study. The first treats both males and females as part of the same hierarchy, even though males and females in the wild will often form separate hierarchies. A separate hierarchy was created by only examining the interactions between females. A separate hierarchy for males was not constructed due to the low number of males in each group. In addition, it was observed that males rarely interacted with females in either primate group. For example, Omoshiroi spent most of his time on the peripheral of the enclosure's island away from the females.

To determine each member's rank, a score was calculated by examining how often a member was spatially displaced when approached by another member, or if a member won or lost in an agonistic encounter. Table 5 details the number of agonistic encounters between spider monkeys and Table 6 details the number of agonistic encounters between the Japanese macaques. A member's rank was given based on a normalized David's score calculated using the EloRating package. A higher score indicates a higher rank. Each member's David's score was calculated by using the formula $DS=w+w_2-l-l_2$ where w is the sum of P_{ji}, w_2 is the sum of w values of the individuals that i interacted with, l represents the sum of I's P_{ji} values, and l_2 represents the summed l values in which individual l interacted with (Gammell et al., 2002, p. 602). $P_{ij}=\alpha_{ij}/n_{ij}$ is the proportion that individual i defeats individual j (α_{ij}) in their interactions divided by the total number of interactions between i and j (n_{ij}), and P_{ji} is $P_{ji}=1-P_{ij}$ (Gammell et al., 2002, p. 602). After calculating David's score, a normalized score is calculated using the formula $NormDS=[DS+MaxDS(N)]/N=[DS+N(N-1)/2]/N$. DS represents David's score, MaxDS is the highest DS obtained in the group, and N is the number of members in the group (Stevens et al., 2005, p. 586). The purpose of normalizing David's score is to create a best fit line with a slope between 1 and 0, with 1 representing a very steep hierarchy (de Vries et al., 2006, p. 586). To determine the hierarchical steepness for each primate group, a fitted line is plotted using each member's normDS value as the Y value and their rank as the X value.



Initiator	Recipient	Species	Approaches	Recipient Supplanted	Aggression
Emily	Kramer	Spider Monkey	16	0	0
Emily	Rosie	Spider Monkey	43	0	0
Emily	Twiggy	Spider Monkey	34	0	0
Kramer	Emily	Spider Monkey	9	1	0
Kramer	Rosie	Spider Monkey	5	0	0
Kramer	Twiggy	Spider Monkey	5	0	0
Rosie	Emily	Spider Monkey	46	1	0
Rosie	Kramer	Spider Monkey	21	0	0
Rosie	Twiggy	Spider Monkey	16	1	0
Twiggy	Emily	Spider Monkey	42	4	0
Twiggy	Kramer	Spider Monkey	14	1	0
Twiggy	Rosie	Spider Monkey	51	7	0

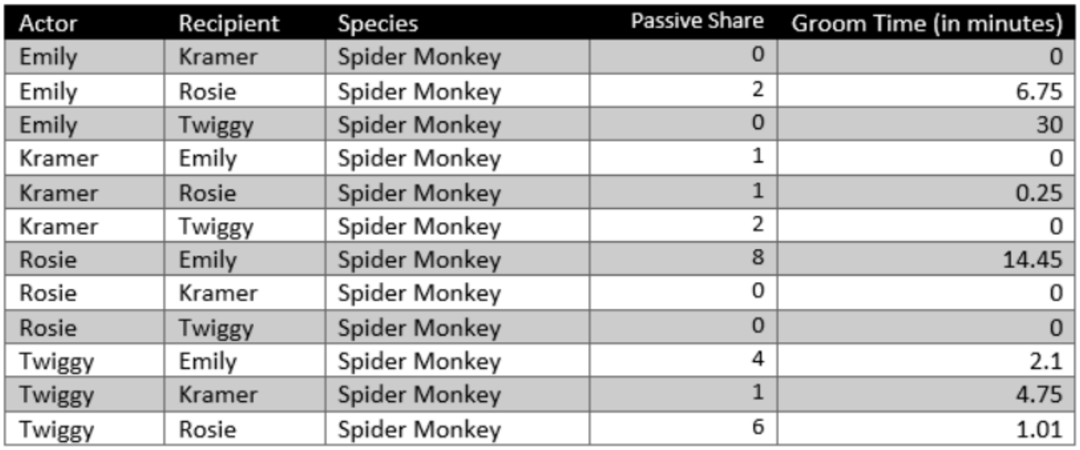
Table 5: Observations of agonistic interactions between dyads within the spider monkey group.

Initiator	Recipient	Species	Approaches	Recipient Supplanted	Aggression
Boggie	Grinch	Japanese Macaque	3	0	0
Boggie	Hedy	Japanese Macaque	3	0	0
Boggie	Kodomo	Japanese Macaque	1	0	0
Boggie	Marlene	Japanese Macaque	9	2	1
Boggie	Omoshiroi	Japanese Macaque	4	0	0
Grinch	Boggie	Japanese Macaque	7	0	0
Grinch	Hedy	Japanese Macaque	13	5	1
Grinch	Kodomo	Japanese Macaque	30	4	1
Grinch	Marlene	Japanese Macaque	8	8	8
Grinch	Omoshiroi	Japanese Macaque	1	0	0
Hedy	Boggie	Japanese Macaque	4	0	0
Hedy	Grinch	Japanese Macaque	10	0	0
Hedy	Kodomo	Japanese Macaque	10	2	0
Hedy	Marlene	Japanese Macaque	11	3	0
Hedy	Omoshiroi	Japanese Macaque	0	0	0
Kodomo	Boggie	Japanese Macaque	8	0	0
Kodomo	Grinch	Japanese Macaque	15	1	0
Kodomo	Hedy	Japanese Macaque	16	9	3
Kodomo	Marlene	Japanese Macaque	20	2	0
Kodomo	Omoshiroi	Japanese Macaque	7	0	0
Marlene	Boggie	Japanese Macaque	5	0	0
Marlene	Grinch	Japanese Macaque	18	1	0
Marlene	Hedy	Japanese Macaque	7	0	0
Marlene	Kodomo	Japanese Macaque	9	1	0
Marlene	Omoshiroi	Japanese Macaque	4	0	0
Omoshiroi	Boggie	Japanese Macaque	4	0	0
Omoshiroi	Grinch	Japanese Macaque	1	0	0
Omoshiroi	Hedy	Japanese Macaque	1	0	0
Omoshiroi	Kodomo	Japanese Macaque	2	1	1
Omoshiroi	Marlene	Japanese Macaque	4	1	1

Table 6: Recorded observations for each time a member of the Japanese Macaque group was spatially supplanted either through an approach or through aggression.

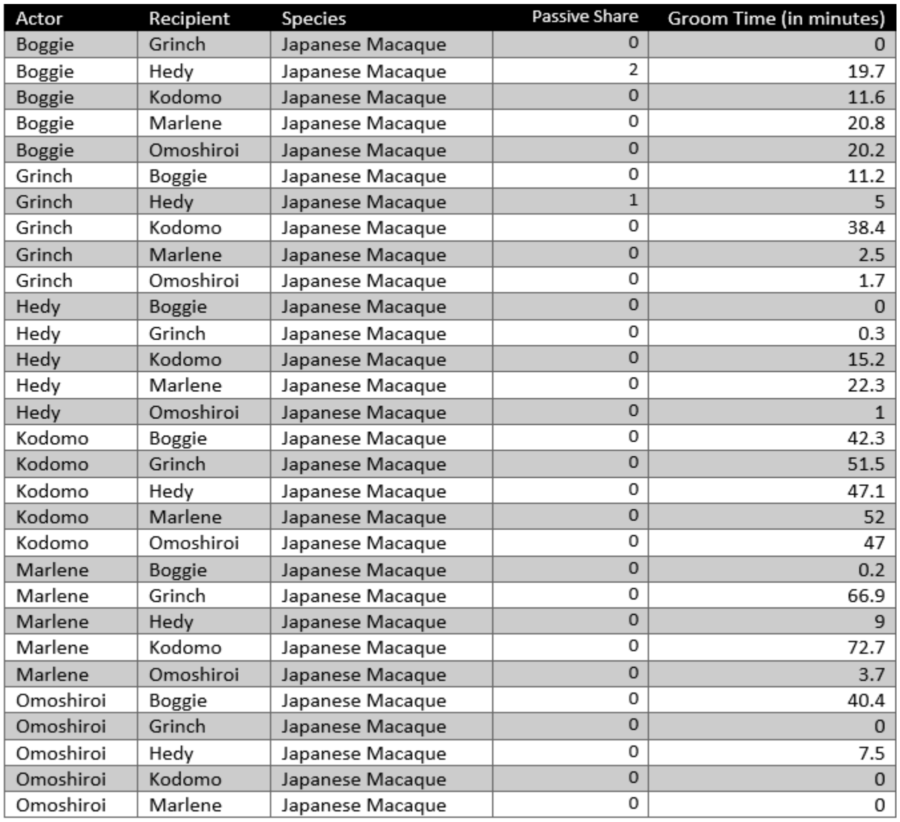
Row-wise correlation tests of actor/receiver matrices were used to test for reciprocity between members. Variables used in actor/receiver matrices are response variables so the data are not independent and we cannot use Pearson's or Kendall's tau statistic (Hemelrijk, 1990). Instead, a row-wise comparison using the Kr test statistic was used to test the matrices using a custom script in r-data to test the relative and absolute reciprocity for each group. A significant result for relative reciprocity would indicate that there is a correlation between the frequency with which an individual shares and the frequency with which that individual receives food or help in another matrix (Hemelrijk, 1990). The hypothesis for absolute reciprocity is that there is reciprocity, but animals have the same baseline level of activity (Hemelrijk, 1990). On the other hand, the hypothesis for relative reciprocity is that there is reciprocity but animals have a different baseline of activity (Hemelrijk, 1990). The null hypothesis for relative reciprocity would be that there is no evidence to support reciprocity between individuals. In that case, there would be no reason to test the absolute reciprocity in the group. The tests are two-tailed and a significant left-sided P-value would indicate a negative correlation while a significant right-sided P-value would indicate a positive correlation (Hemelrijk, 1990).

This study tested for a correlation between grooming that an individual gave and grooming an individual received. Tests were also performed to see if there was a relationship between grooming given and food received from sharing. I also tested for a relationship between the food given and food received. The actor/receiver matrices for the spider monkeys were constructed using the data from Table 7, and the actor/receiver matrices for the Japanese macaques were constructed using the data from Table 8. The matrices for the grooming an individual received and the food an individual received were made by making a transposed matrix of the food given or grooming given matrices.



Actor	Recipient	Species	Passive Share	Groom Time (in minutes)
Emily	Kramer	Spider Monkey	0	0
Emily	Rosie	Spider Monkey	2	6.75
Emily	Twiggy	Spider Monkey	0	30
Kramer	Emily	Spider Monkey	1	0
Kramer	Rosie	Spider Monkey	1	0.25
Kramer	Twiggy	Spider Monkey	2	0
Rosie	Emily	Spider Monkey	8	14.45
Rosie	Kramer	Spider Monkey	0	0
Rosie	Twiggy	Spider Monkey	0	0
Twiggy	Emily	Spider Monkey	4	2.1
Twiggy	Kramer	Spider Monkey	1	4.75
Twiggy	Rosie	Spider Monkey	6	1.01

Table 7: Observations of passive sharing and grooming between dyads of spider monkeys.

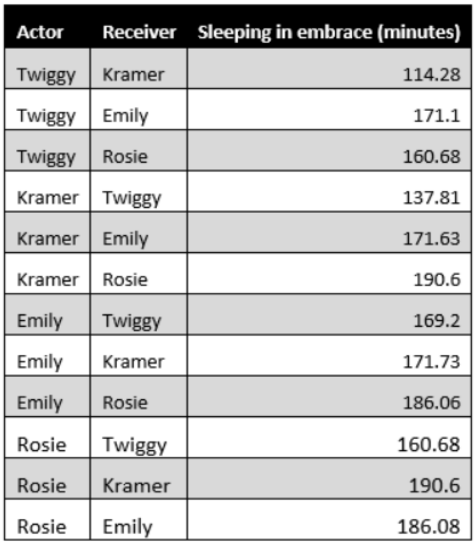


Actor	Recipient	Species	Passive Share	Groom Time (in minutes)
Boggie	Grinch	Japanese Macaque	0	0
Boggie	Hedy	Japanese Macaque	2	19.7
Boggie	Kodomo	Japanese Macaque	0	11.6
Boggie	Marlene	Japanese Macaque	0	20.8
Boggie	Omoshiroi	Japanese Macaque	0	20.2
Grinch	Boggie	Japanese Macaque	0	11.2
Grinch	Hedy	Japanese Macaque	1	5
Grinch	Kodomo	Japanese Macaque	0	38.4
Grinch	Marlene	Japanese Macaque	0	2.5
Grinch	Omoshiroi	Japanese Macaque	0	1.7
Hedy	Boggie	Japanese Macaque	0	0
Hedy	Grinch	Japanese Macaque	0	0.3
Hedy	Kodomo	Japanese Macaque	0	15.2
Hedy	Marlene	Japanese Macaque	0	22.3
Hedy	Omoshiroi	Japanese Macaque	0	1
Kodomo	Boggie	Japanese Macaque	0	42.3
Kodomo	Grinch	Japanese Macaque	0	51.5
Kodomo	Hedy	Japanese Macaque	0	47.1
Kodomo	Marlene	Japanese Macaque	0	52
Kodomo	Omoshiroi	Japanese Macaque	0	47
Marlene	Boggie	Japanese Macaque	0	0.2
Marlene	Grinch	Japanese Macaque	0	66.9
Marlene	Hedy	Japanese Macaque	0	9
Marlene	Kodomo	Japanese Macaque	0	72.7
Marlene	Omoshiroi	Japanese Macaque	0	3.7
Omoshiroi	Boggie	Japanese Macaque	0	40.4
Omoshiroi	Grinch	Japanese Macaque	0	0
Omoshiroi	Hedy	Japanese Macaque	0	7.5
Omoshiroi	Kodomo	Japanese Macaque	0	0
Omoshiroi	Marlene	Japanese Macaque	0	0

Table 8: Observations of passive sharing and grooming between dyads of Japanese macaques

I explored if exchanges were affected by rank. Row-wise correlation tests were performed on grooming actor/receiver matrices along with actor/receiver matrices based on rank. Rank matrices were constructed by ordering members from the highest rank to the lowest within an actor/receiver matrix and assigning the highest ranked individual the highest number in their column. Zeros were assigned where a member's column intersected with his or her own respective row within the matrix. A significant right-sided p-value would indicate that members exchange either grooming or food by rank. If a significant p-value was found, a separate partial matrix test was to be performed to control for the influences on rank.

For black-handed spider monkeys, I also tested for a correlation between how often individuals exchanged food or grooming and how often they slept in each other's embrace (Table 9). Black-handed spider monkeys spent a significant amount of time sleeping in an embrace with one another. The study did not test to determine if there would be reciprocity of sleeping by comparing a transposed matrix of sleeping. This is because there is not an actor/receiver relationship with sleeping.



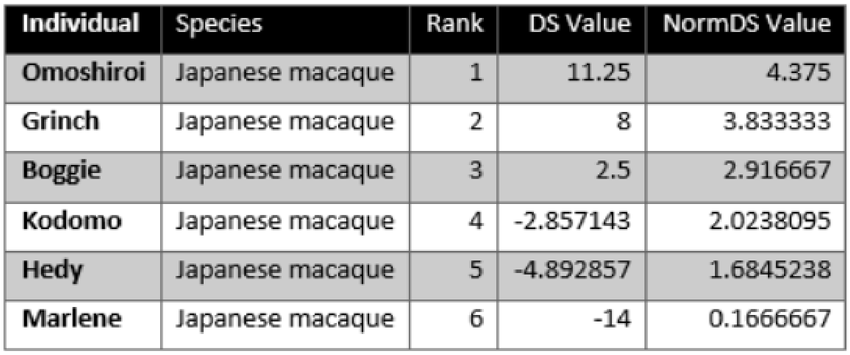
Actor	Receiver	Sleeping in embrace (minutes)
Twiggy	Kramer	114.28
Twiggy	Emily	171.1
Twiggy	Rosie	160.68
Kramer	Twiggy	137.81
Kramer	Emily	171.63
Kramer	Rosie	190.6
Emily	Twiggy	169.2
Emily	Kramer	171.73
Emily	Rosie	186.06
Rosie	Twiggy	160.68
Rosie	Kramer	190.6
Rosie	Emily	186.08

Table 9: Observed time in minutes each member slept with another member in an embrace

Results and Discussion

<u>Hierarchy</u>

The steepness for the Japanese macaques was calculated using the DS values found in Table 10. The steepness for the black-handed spider monkeys was calculated using the DS values found in Table 11. A second proposed hierarchy focusing only on the interactions between Japanese macaque females was created using the values found in Table 12, and the proposed hierarchy focusing only on interactions between spider monkey females was created using the values found in Table 13.

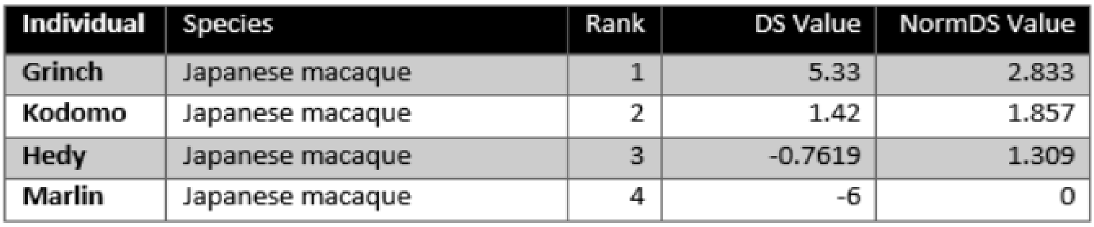


Individual	Species	Rank	DS Value	NormDS Value
Omoshiroi	Japanese macaque	1	11.25	4.375
Grinch	Japanese macaque	2	8	3.833333
Boggie	Japanese macaque	3	2.5	2.916667
Kodomo	Japanese macaque	4	-2.857143	2.0238095
Hedy	Japanese macaque	5	-4.892857	1.6845238
Marlene	Japanese macaque	6	-14	0.1666667

Table 10: The calculated DS value, rank, and normDS value for the Japanese macaques.

Individual	Species	Rank	DS Value	NormDS Value
Kramer	Black-Handed Spider Monkey	1	2	2
Emily	Black-Handed Spider Monkey	2	1.46667	1.8667
Twiggy	Black-Handed Spider Monkey	3	0.6285714	1.6571429
Rosie	Black-Handed Spider Monkey	4	-4.0952381	0.4761905

Table 11: The calculated DS value, rank, and normDS value for the black-handed spider monkeys.



Individual	Species	Rank	DS Value	NormDS Value
Grinch	Japanese macaque	1	5.33	2.833
Kodomo	Japanese macaque	2	1.42	1.857
Hedy	Japanese macaque	3	-0.7619	1.309
Marlin	Japanese macaque	4	-6	0

Table 12: The calculated DS value, rank, and NormDs value of the Japanese macaques if females are treated as having separate hierarchies.

Individual	Species	Rank	DS Value	NormDS Value
Twiggy	Black-Handed Spider Monkey	1	1.97	1.657
Emily	Black-Handed Spider Monkey	2	-0.4	0.86
Rosie	Black-Handed Spider Monkey	3	-1.571	0.47616

Table 13: The calculated DS value, rank, and NormDS value of the Black-Handed Spider monkeys if females are treated as having separate hierarchies.

Japanese Macaques

The proposed hierarchy of males and females for the Japanese macaques had a slope of -0.81 and a p-value of 0.000239 (F=155.3, df=1,11) (Table 14). However, if we calculate the hierarchy with just the females (Figure 4), we can see that hierarchy is slightly steeper with a slope of -0.90 and a p-value 0.011 (F=83.17, df=1,2). The slope coefficients of -0.81 and -0.90 indicates that each hierarchy is very steep. This fits with the predicted hierarchy for Japanese macaques as they normally form steep matrilineal hierarchies in wild populations. The difference between the steepness for each group might be explained by the small sample size of dyadic encounters. During the study, the Japanese macaques were often not observed forming coalitions, but there were two instances of affiliative behavior. Both times, Grinch assisted Kodomo in fights. The first fight was between Hedy and Kodomo. Kodomo overpowered Hedy by throwing her into the pond with Grinch while Marlene bit Hedy. The second fight was one of the few interactions Omoshiroi had with the females. Omoshiroi

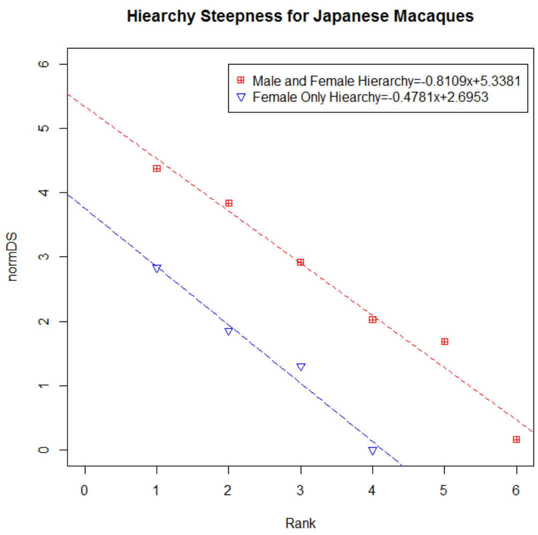
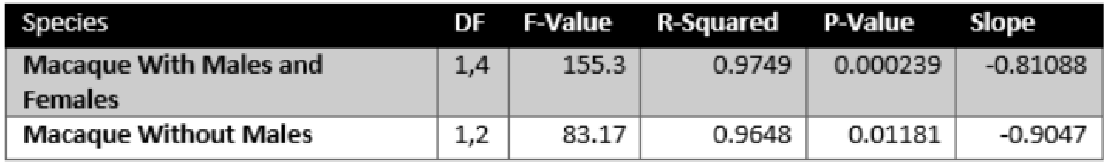


Figure 4: Steepness for each proposed Japanese macaque hierarchy.

attempted to chase Kodomo away when she was crossing Omoshiroi's path. Grinch came to Kodomo's aid during this conflict. Despite the aid from Grinch, Omoshiroi was able to chase both Kodomo and Grinch away. Due to the small population size and small data set a test for an association between members' rank and received affiliative behaviors was not performed.



Species	DF	F-Value	R-Squared	P-Value	Slope
Macaque With Males and Females	1,4	155.3	0.9749	0.000239	-0.81088
Macaque Without Males	1,2	83.17	0.9648	0.01181	-0.9047

Table 14: Calculated steepness for the two proposed Japanese macaque hierarchies.

Black-Handed Spider Monkeys

The proposed hierarchy with both males and females has a steepness of -0.47 with a p-value of 0.1144 (F=7.269, df=1,2) (Table 15). When females are treated as forming a separate hierarchy (Figure 5) steepness is -0 .59 with a P-value of=0.1233 (F=25.99, df=1,1). In both cases, the results are not statistically significant at an alpha value of 0.05. Despite the non-significance, members in the male and female hierarchy had similar normDS values with the exception of Rosie. In the slightly steeper all-female hierarchy member ranks change. Twiggy is the highest ranked member of the all-female group, but Emily is ranked higher

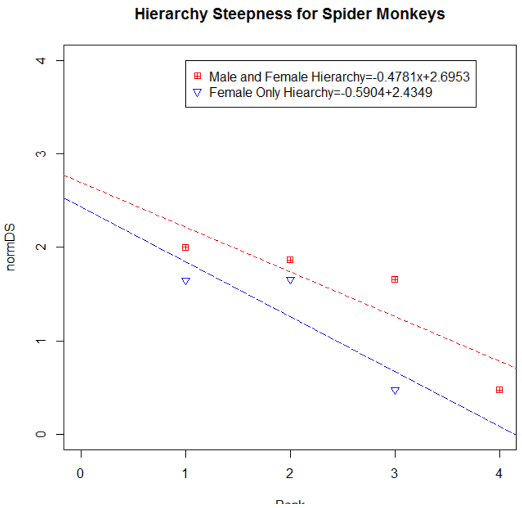
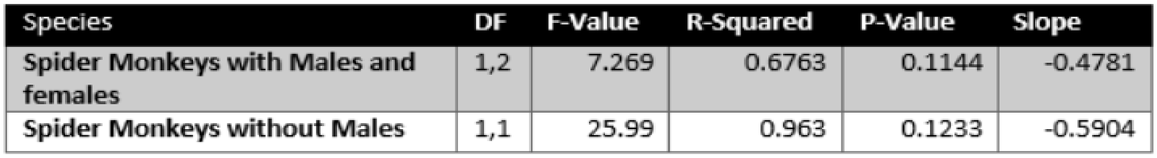


Figure 5: Steepness for each proposed Spider monkey hierarchy.

than Twiggy in the hierarchy that includes males. This could be explained by the fact that Kramer only interacted with his sister Emily.



Species	DF	F-Value	R-Squared	P-Value	Slope
Spider Monkeys with Males and females	1,2	7.269	0.6763	0.1144	-0.4781
Spider Monkeys without Males	1,1	25.99	0.963	0.1233	-0.5904

Table 15: Calculated steepness for the two hypothetical black-handed spider monkey hierarchies.

One likely explanation for the non-significant p-value is that there are only four members of the group, and the only male in the group rarely interacted with the others. Thus, there are not enough data points to create a stable hierarchy. Another explanation is the relatively few agonistic encounters recorded in comparison to the total approaches. There were 302 recorded approaches and only 15 occurrences of a member being supplanted. This means that only 4.9% of approaches resulted in a member being supplanted. In the Japanese macaque group there were 157 approaches with 21 (13.3%) supplants (Figure 6).

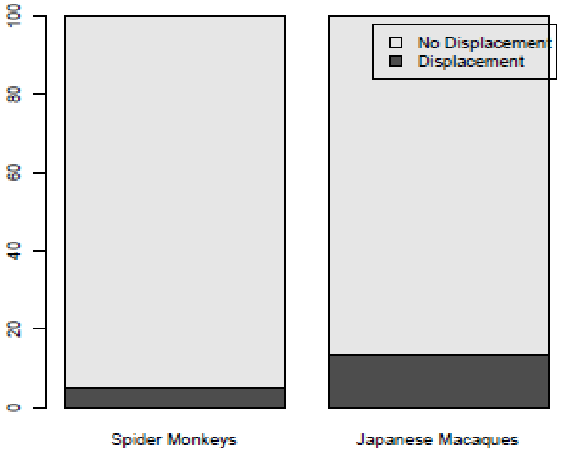


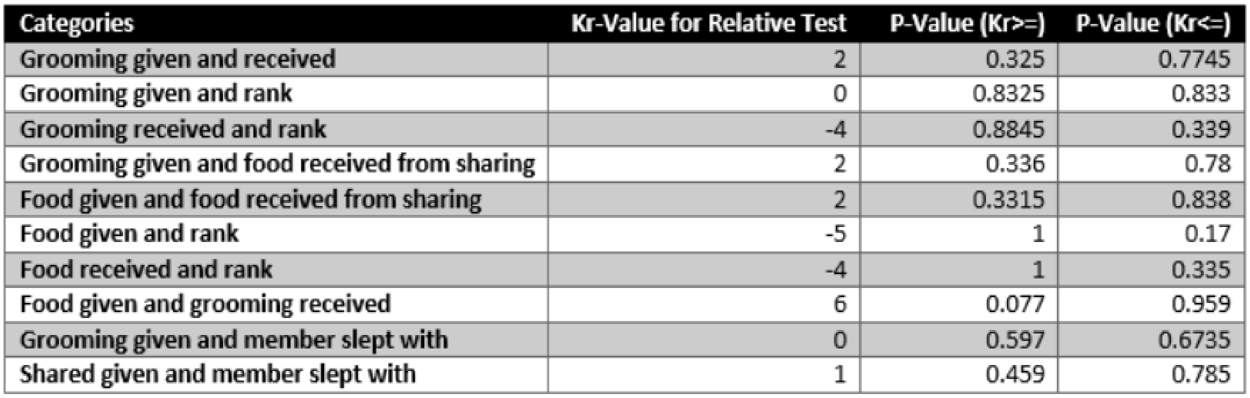
Figure 6: Comparison of percentage of times members displaced through aggression or supplanted when approached between spider monkeys and macaques.

Species and displacement are not independent (X^2=8.9756, df=1, p-value = 0.0027). Japanese macaques are characterized by significantly more agonistic encounters than black-handed spider monkeys. The lack of agonistic encounters between spider monkeys could explain the non-significant results of the test for hierarchy and could suggest that the spider monkeys' hierarchy is not stable. The fewer agonistic encounters could indicate a more egalitarian group, with little enforcement of rank.

Reciprocity

Black-Handed Spider Monkeys

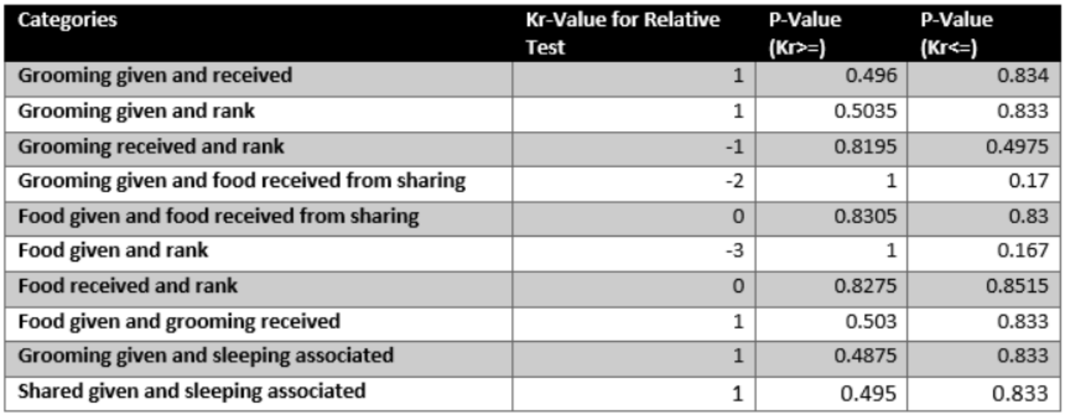
Row-wise correlation tests were used to test for reciprocity among black-handed spider monkeys. All tests of reciprocity in the hierarchy containing both sexes were all not statistically significant (Table 16), indicating neither positive nor negative reciprocity for any of the behavioral categories. The results for the female-only hierarchy were also not significant. (Table 17). The non-significant results suggest that there is no evidence for reciprocity among females, and no additional tests were done to see if there was an absolute reciprocity.



Categories	Kr-Value for Relative Test	P-Value (Kr>=)	P-Value (Kr<=)
Grooming given and received	2	0.325	0.7745
Grooming given and rank	0	0.8325	0.833
Grooming received and rank	-4	0.8845	0.339
Grooming given and food received from sharing	2	0.336	0.78
Food given and food received from sharing	2	0.3315	0.838
Food given and rank	-5	1	0.17
Food received and rank	-4	1	0.335
Food given and grooming received	6	0.077	0.959
Grooming given and member slept with	0	0.597	0.6735
Shared given and member slept with	1	0.459	0.785

Table 16: Kr tests for relative reciprocity among the black-handed spider monkeys group if females and males were considered as forming one hierarchy.

The non-significant results for reciprocity revealed that grooming, the sharing of food, and which individuals slept in an embrace were not influenced by their rank. Partial row-wise correlations were not used to control for rank due to lack of significance between rank and reciprocity. The lack of significance for a positive reciprocity between grooming and sharing does not suggest evidence of reciprocity between members. However, the lack of significance also suggests there is not a directionality of grooming or sharing from subordinate to dominant.

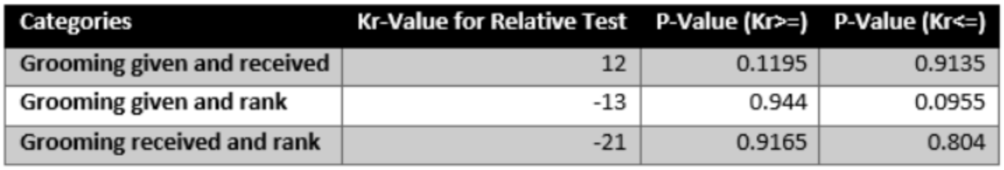


Categories	Kr-Value for Relative Test	P-Value (Kr>=)	P-Value (Kr<=)
Grooming given and received	1	0.496	0.834
Grooming given and rank	1	0.5035	0.833
Grooming received and rank	-1	0.8195	0.4975
Grooming given and food received from sharing	-2	1	0.17
Food given and food received from sharing	0	0.8305	0.83
Food given and rank	-3	1	0.167
Food received and rank	0	0.8275	0.8515
Food given and grooming received	1	0.503	0.833
Grooming given and sleeping associated	1	0.4875	0.833
Shared given and sleeping associated	1	0.495	0.833

Table 17: Kr tests for relative reciprocity among the black-handed spider monkeys group if females are considered as having a separate hierarchy.

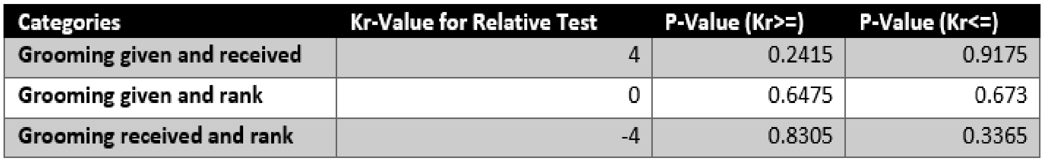
Japanese Macaques

Row-wise correlation of actor/receiver matrices were also used to test for reciprocity among Japanese macaques. There were only three instances of food sharing between members, and case involved the same piece of rope that Hedy, Grinch, and Boggie were eating. Tests for reciprocity for food sharing could not be conducted with so few cases. I tested for correlation between grooming given and received for the proposed hierarchy that consists of both males and females (Table 18). I also tested for a correlation between grooming rank. None of the tests achieved statistical significance, meaning that tests for absolute reciprocity were not performed. Tests for negative reciprocity were also not significant. These results indicate that there is no evidence of reciprocity of grooming. They also indicate that grooming is not directed unilaterally towards dominants from subordinates. The same conclusions are suggested by the tests run on the female-only hierarchy, none of which are statistically significant (Table 19).



Categories	Kr-Value for Relative Test	P-Value (Kr>=)	P-Value (Kr<=)
Grooming given and received	12	0.1195	0.9135
Grooming given and rank	-13	0.944	0.0955
Grooming received and rank	-21	0.9165	0.804

Table 18: Kr tests results among Japanese macaques if males and females are part of the same hierarchy.



Categories	Kr-Value for Relative Test	P-Value (Kr>=)	P-Value (Kr<=)
Grooming given and received	4	0.2415	0.9175
Grooming given and rank	0	0.6475	0.673
Grooming received and rank	-4	0.8305	0.3365

Table 19: Kr tests results among Japanese macaques if females are treated as having a separate hierarchy.

The non-significant results for each K_r tests indicated that there was no evidence for reciprocity in exchanges of grooming. There was no evidence that exchanges of grooming was influenced by either aggression or rank. In addition, there was no evidence of negative reciprocity for each group.

Chapter 6: Conclusions

This research hypothesized that there would be a negative correlation between hierarchy steepness and the frequency of cooperation. Additional research questions asked if the exchanges of food and grooming would flow uniformly from subordinates to dominants in despotic hierarchies, while the flow would be less uniform in more egalitarian hierarchies. Neither hypothesis was supported by the results of the study.

The results of my study cannot be seen as definitive due to a combination of small sample sizes and limited observational time (40 hours for Black-handed spider monkeys and 68.7 hours for Japanese Macaques). More definitive results would be obtained with a longer study involving larger groups. The failure to discover evidence of cooperative behavior in the form of reciprocal exchanges may also be the result of the environments of the groups. The spider monkeys were each supplied with one or more of their own enrichment containers in their enclosure. The keepers of the Japanese macaques avoided provisioning piles of foods in the open to avoid conflicts. In both cases, keeper management techniques were used to discourage intragroup competition, perhaps removing the need for cooperation. As Pansini (2011) pointed out, the introduction of shareable resources with the need to cooperate can reinforce rank dominance. Each member had equal access to all food resources available to the group and there was no need for members to trade to get the resources they needed. Thus, members did not need to use grooming to form relationships to maintain their rank.

Although there was no evidence of cooperation through reciprocity or directionality of exchanges there were differences between the two groups. While displacements were observed among the black-handed spider monkeys there were no instances of aggressive displays or fighting between members. In contrast, the Japanese macaques had noticeably higher occurrences of displacement and aggression. Members of the black-handed spider monkey group were far more tolerant of each other than the Japanese macaques. While the spider monkeys did not engage in reciprocal behavior, they did allow other members to take food freely out of their own enrichment containers or to co-feed out of the same container. The Japanese macaques had three instances of item sharing and one recorded attempt of theft when Hedy made a failed attempt to steal an unidentified plant root from Boggie. The higher frequency of aggression and antagonism among the Japanese macaques suggests that the Japanese macaques are more willing to employ harassment as a strategy to obtain food or desired items.

Another problem with this research is the small number of males in each group. In the wild, males and females will form separate hierarchies. The investigation observed cooperative behavior by including both males and females in the same hierarchy. I did analyze female-only hierarchies, because males rarely interacted with females in either group study. However, there were not enough males in either group to construct a separate male hierarchy. This is unfortunate because the shallow slope of the spider monkey mixed-sex hierarchy hints that spider monkey males do not exhibit a traditional linear hierarchy.

Traditionally, egalitarian groups are defined by a non-linear dominance ranking with a shallow slope, but such an understanding of egalitarian groups compared to despotic groups may be too simplistic. Christopher Boehm argues that egalitarian groups are actually hierarchies based on anti-hierarchical attitudes (Boehm, 1999). This may be true for primate species such as chimpanzees where male-bonded groups compete directly and aggression is frequent. Thus, aggression and displacement can be used to track a member's rank. For non-linear groups like the black-handed spider monkey, there may be an absence of aggression between conspecifics. The group of spider monkeys studied in the group was marked by a lack of aggression. The use of violence to maintain a priority of access may not characterize the social dynamics of all non-linear hierarchies. Network analysis might be more effective in capturing the non-linear hierarchal social structure of a species like the black-handed spider monkeys (Ramos-Fernandez et al.2009).

The next step in this research would be to compare larger groups of macaques and spider monkeys in the wild. The hierarchies of black-handed spider monkeys and Japanese macaques in captivity may differ from the hierarchies found in the wild. As a result, the way these animals cooperate may be different as well. The type of competition that animals face in the wild is a driving factor in how they form their social groups. In a zoo setting, food is provisioned and members do not have to engage in contest competition. Keepers also use techniques to reduce competition and aggression in the group. In addition, nepotism may not be an important factor for both species in a captive setting. Female Japanese macaques may not be related to each other and matrilines may not form. The absence of a female matriline hierarchy could result in cooperation between unrelated females or any hierarchy formed between females may be egalitarian. Male Japanese macaques may be able to exert more dominance over females who lack support from related females.

Without competition between members, there may not be a reason for conspecifics to cooperate to get access to preferred food or reproduction. There may be no clear pattern of cooperation if the hierarchy is unclear and there is no need for cooperation in either species.

Grooming and exchanges of food may not be directed asymmetrically towards dominant from subordinate, but there may also be no evidence for reciprocity of cooperative behavior.

In a wild setting, the lack of provisioned food may increase the need for cooperation due to the increased potential for competition between members. Traditional measures of linearity should be complemented with network analysis to examine association between members.

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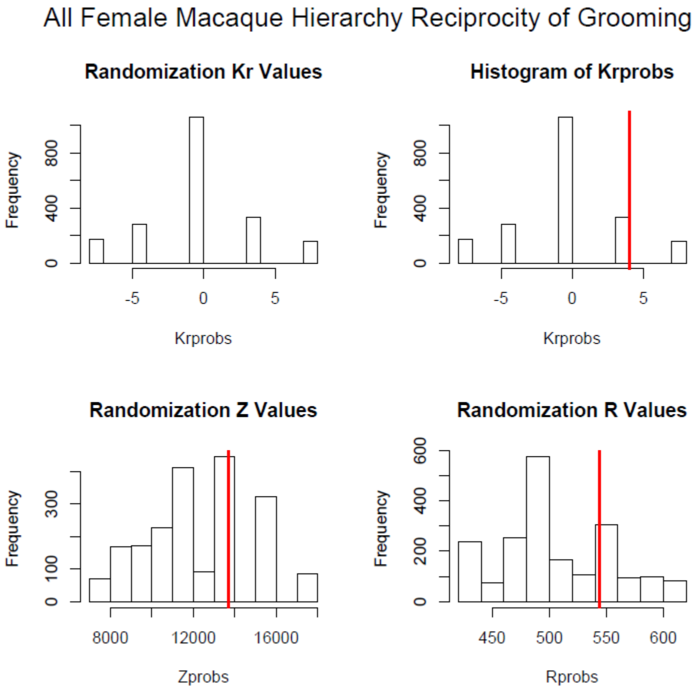
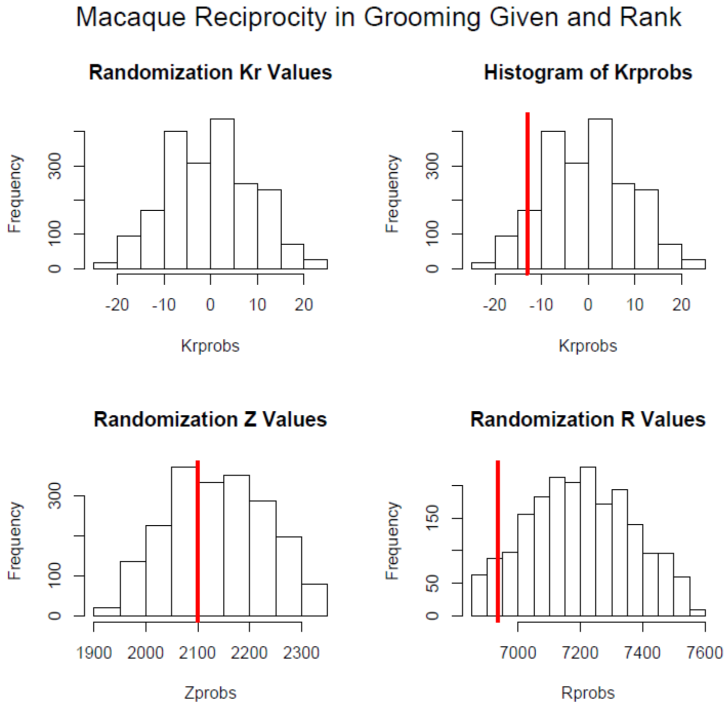
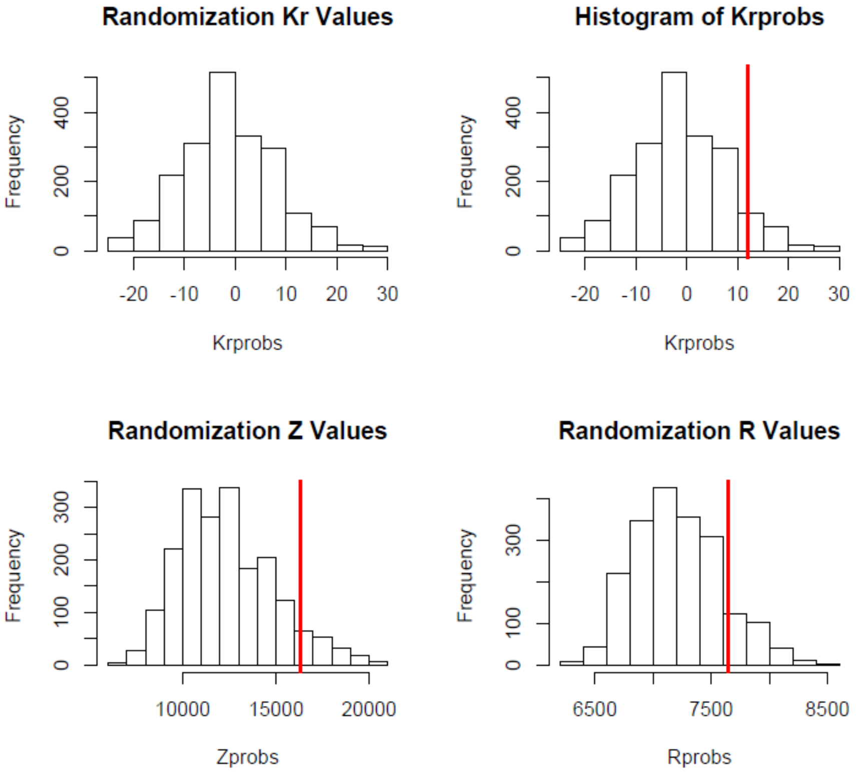
Appendix A

Japanese macaque probability distribution graphs for each tests of relative reciprocity and absolute reciprocity.

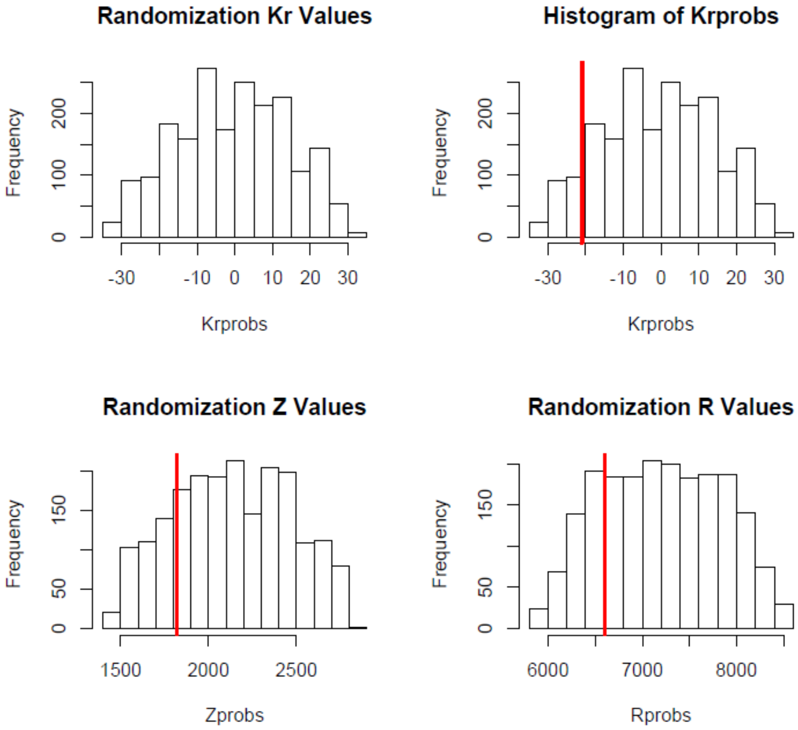




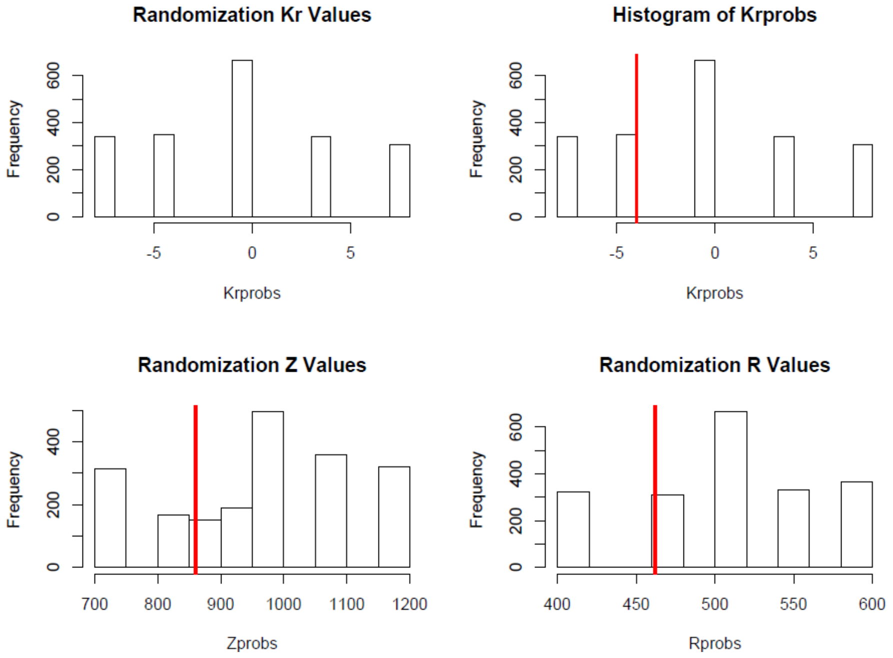
Macaque Reciprocity of Grooming



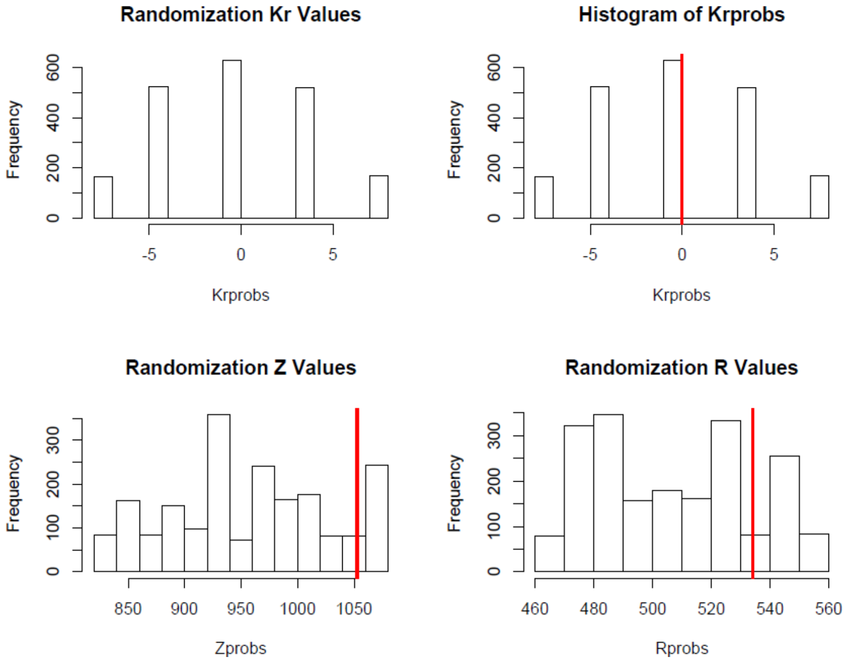
Macaque Reciprocity in Regards Received Grooming and Rank



All Female Macaque Hierarchy Reciprocity of Grooming Received and Rank

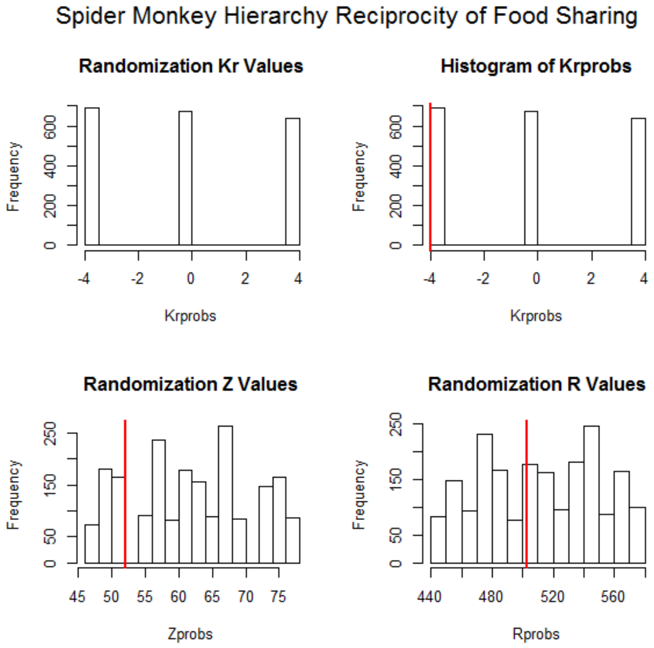


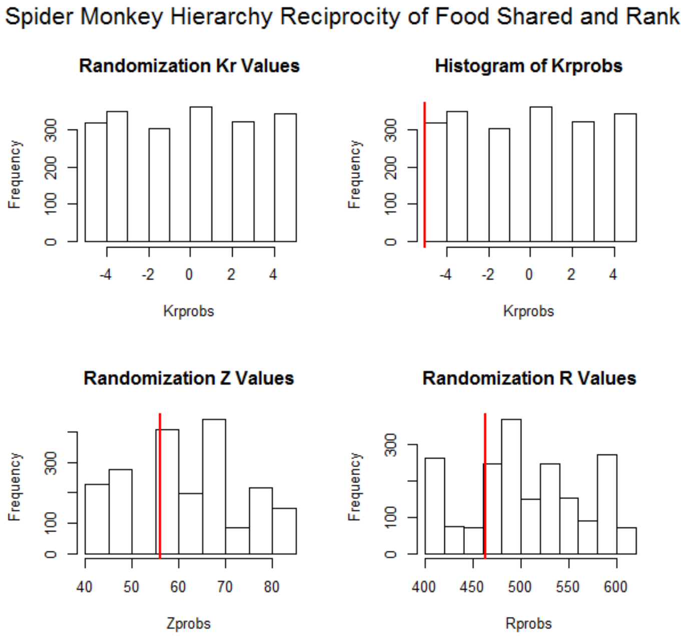
All Female Macaque Hierarchy Reciprocity of Grooming Given and Rank

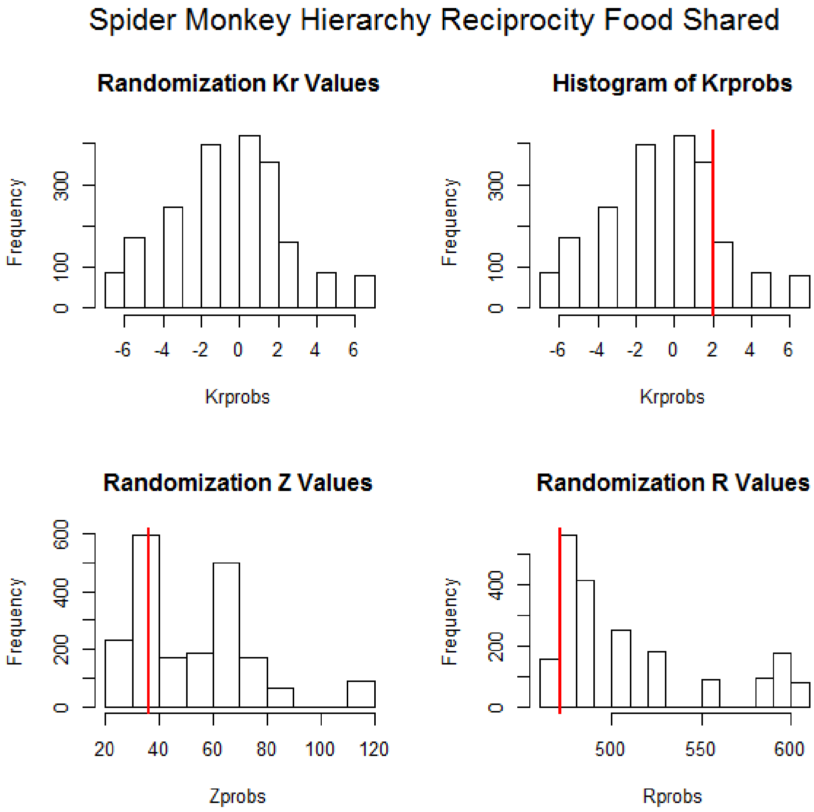


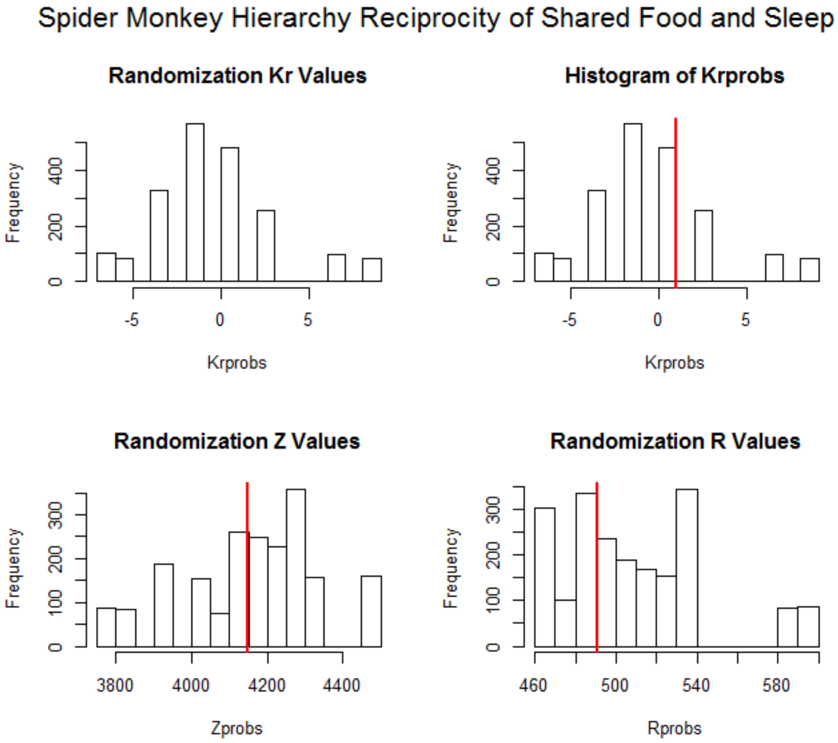
Appendix B

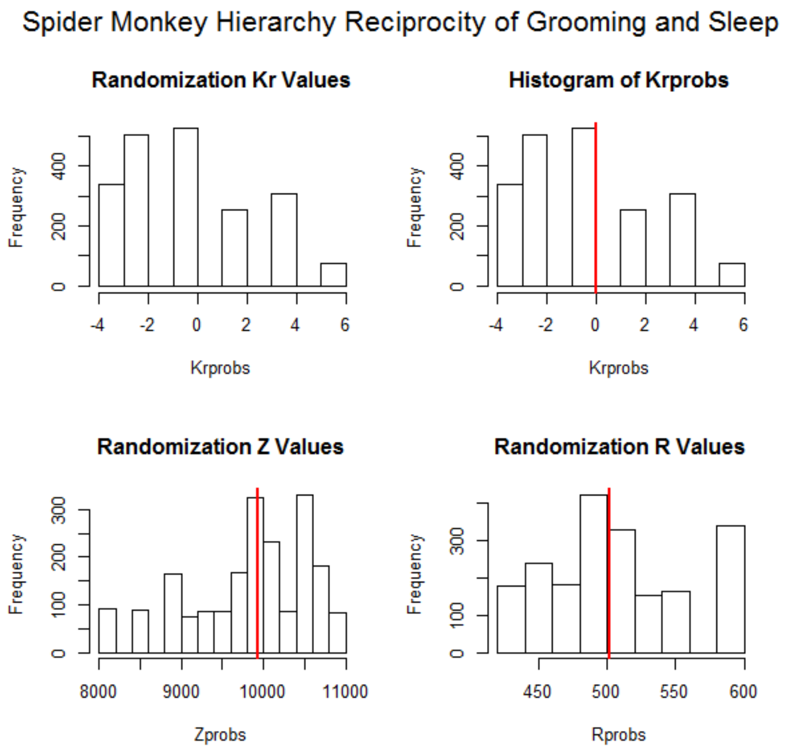
Black-handed spider monkey probability distribution graphs for each tests of relative reciprocity and absolute reciprocity.

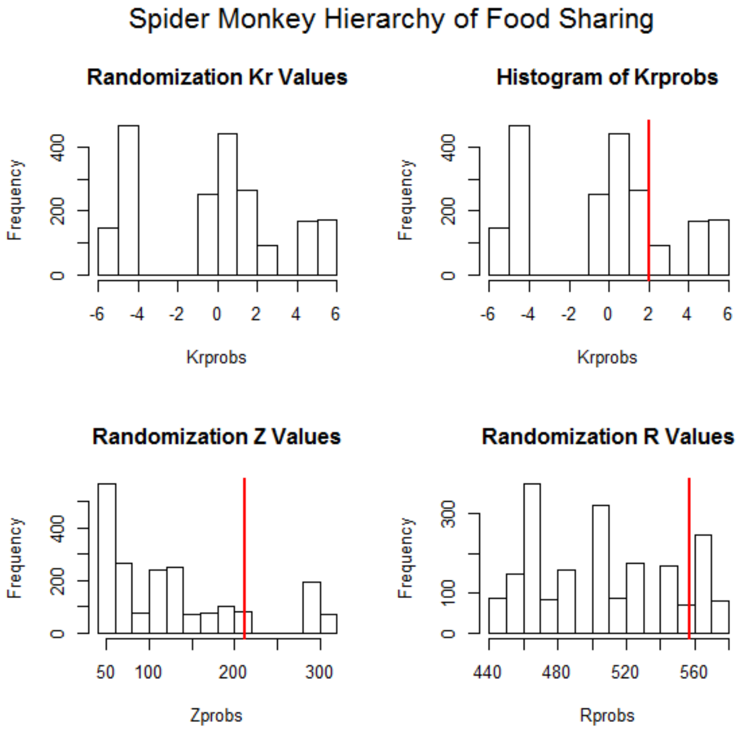


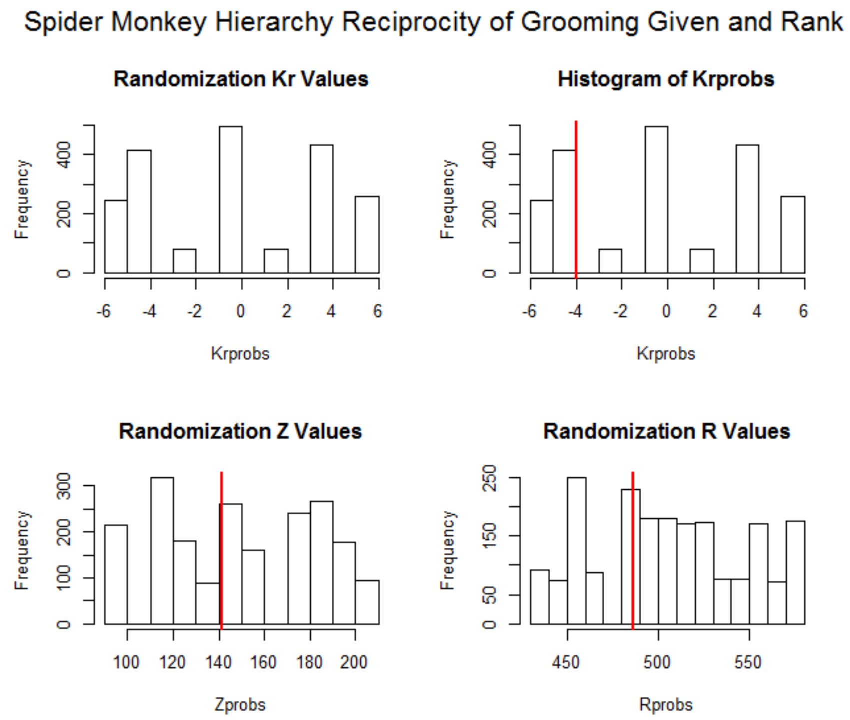


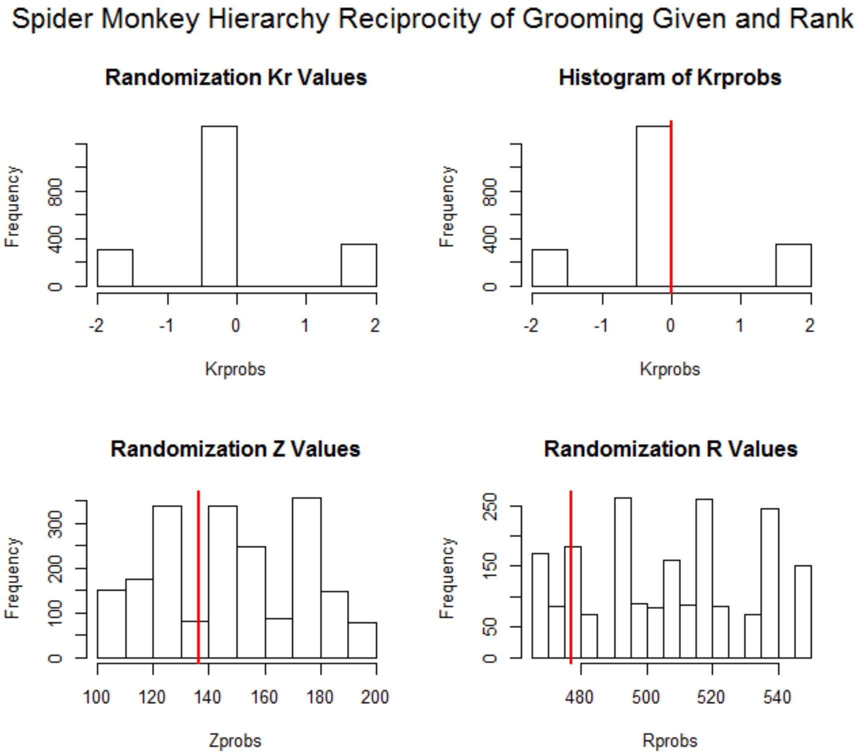

Spider Monkey Hierarchy Reciprocity Food Shared
Randomization Kr Values
Frequency
0
100
300
-6
-4
-2
0
2
4
6
Krprobs
Histogram of Krprobs
Frequency
0
100
300
-6
-4
-2
0
2
4
6
Krprobs
Randomization Z Values
Frequency
0
200
400
600
20
40
60
80
100
120
Zprobs
Randomization R Values
Frequency
0
200
400
500
550
600
Rprobs

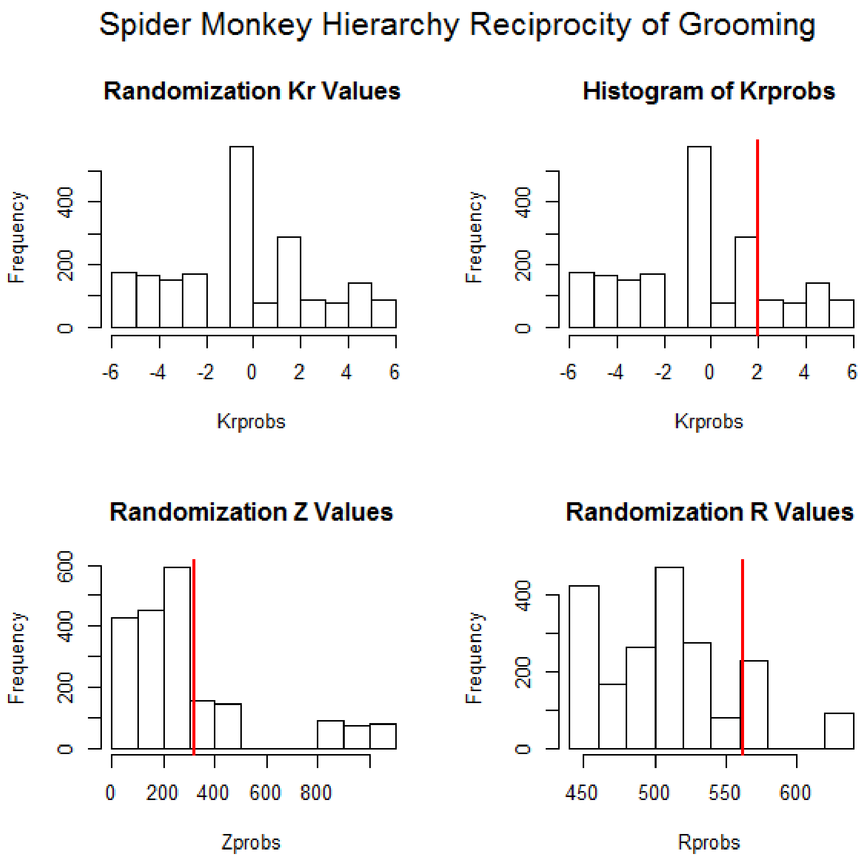

Spider Monkey Hierarchy Reciprocity of Shared Food and Sleep
Randomization Kr Values
Frequency
0
200
400
-5
0
5
Krprobs
Histogram of Krprobs
Frequency
0
200
400
-5
0
5
Krprobs
Randomization Z Values
Frequency
0
100
200
300
3800
4000
4200
4400
Zprobs
Randomization R Values
Frequency
0
100
200
300
460
500
540
580
Rprobs

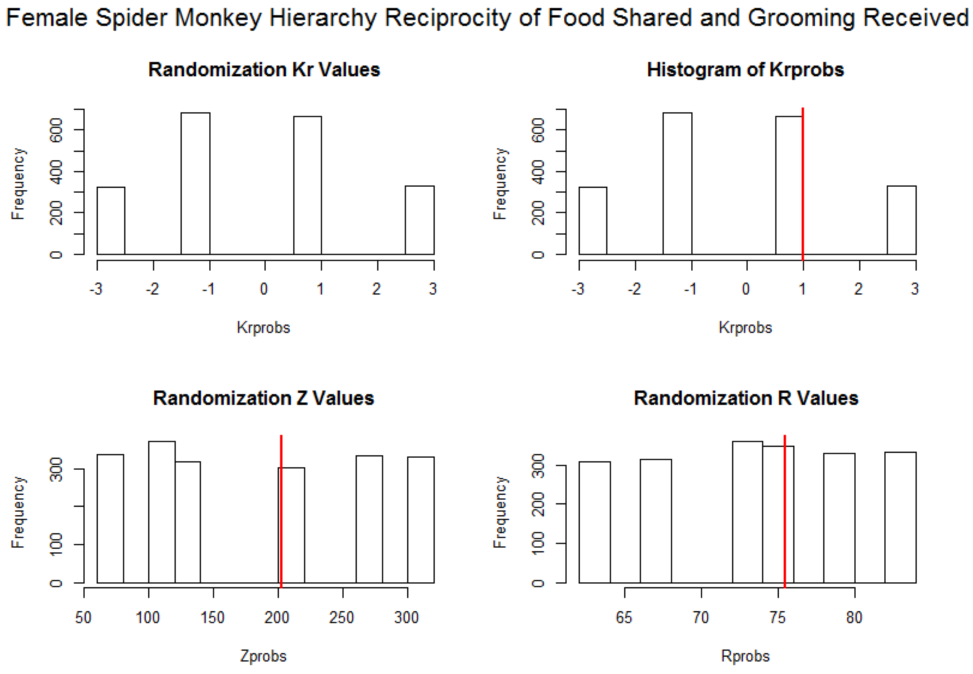

Spider Monkey Hierarchy Reciprocity of Grooming and Sleep
Randomization Kr Values
Frequency
0
200
400
-4
-2
0
2
4
6
Krprobs
Histogram of Krprobs
Frequency
0
200
400
-4
-2
0
2
4
6
Krprobs
Randomization Z Values
Frequency
0
100
200
300
8000
9000
10000
11000
Zprobs
Randomization R Values
Frequency
0
100
300
450
500
550
600
Rprobs


Spider Monkey Hierarchy of Food Sharing
Randomization Kr Values
Frequency
0
200
400
-6
-4
-2
0
2
4
6
Krprobs
Histogram of Krprobs
Frequency
0
200
400
-6
-4
-2
0
2
4
6
Krprobs
Randomization Z Values
Frequency
0
200
400
50
100
200
300
Zprobs
Randomization R Values
Frequency
0
100
300
440
480
520
560
Rprobs

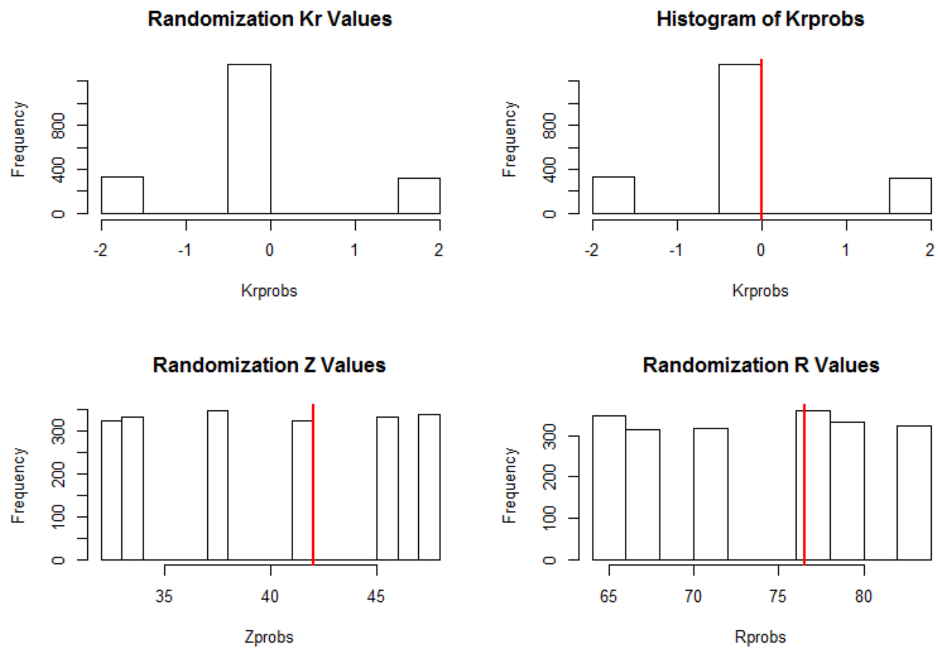

Spider Monkey Hierarchy Reciprocity of Grooming Given and Rank
Randomization Kr Values
Frequency
0
200
400
-6
-4
-2
0
2
4
6
Krprobs
Histogram of Krprobs
Frequency
0
200
400
-6
-4
-2
0
2
4
6
Krprobs
Randomization Z Values
Frequency
0
100
200
300
100
120
140
160
180
200
Zprobs
Randomization R Values
Frequency
0
50
150
250
450
500
550
Rprobs


Spider Monkey Hierarchy Reciprocity of Grooming Given and Rank
Randomization Kr Values
Frequency
0
400
800
-2
-1
0
1
2
Krprobs
Histogram of Krprobs
Frequency
0
400
800
-2
-1
0
1
2
Krprobs
Randomization Z Values
Frequency
0
100
200
300
100
120
140
160
180
200
Zprobs
Randomization R Values
Frequency
0
50
150
250
480
500
520
540
Rprobs

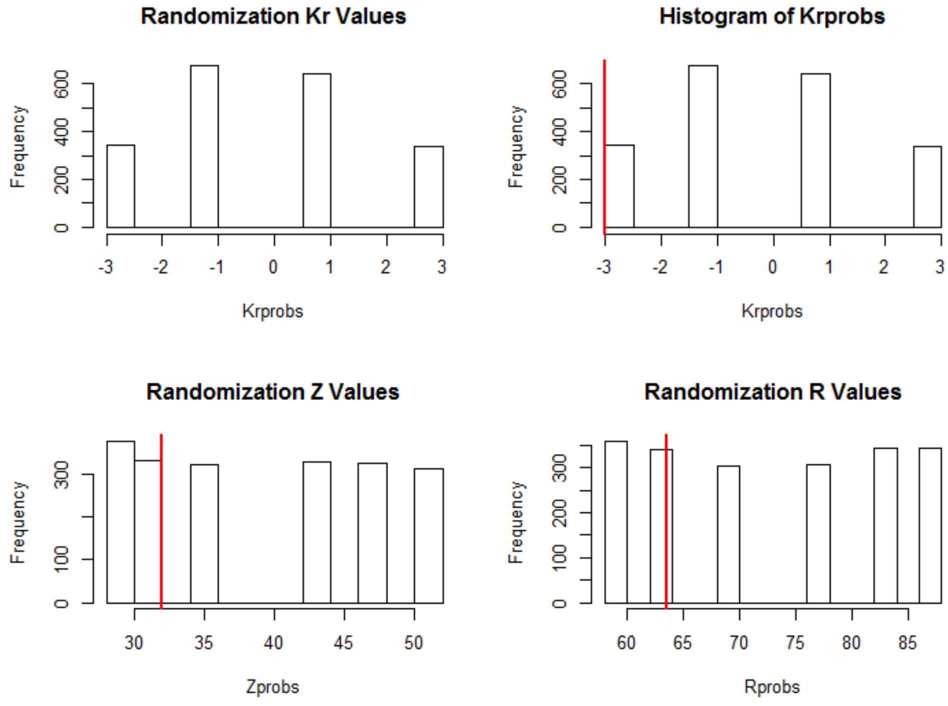

Spider Monkey Hierarchy Reciprocity of Grooming


Female Spider Monkey Hierarchy Reciprocity of Food Shared and Grooming Received

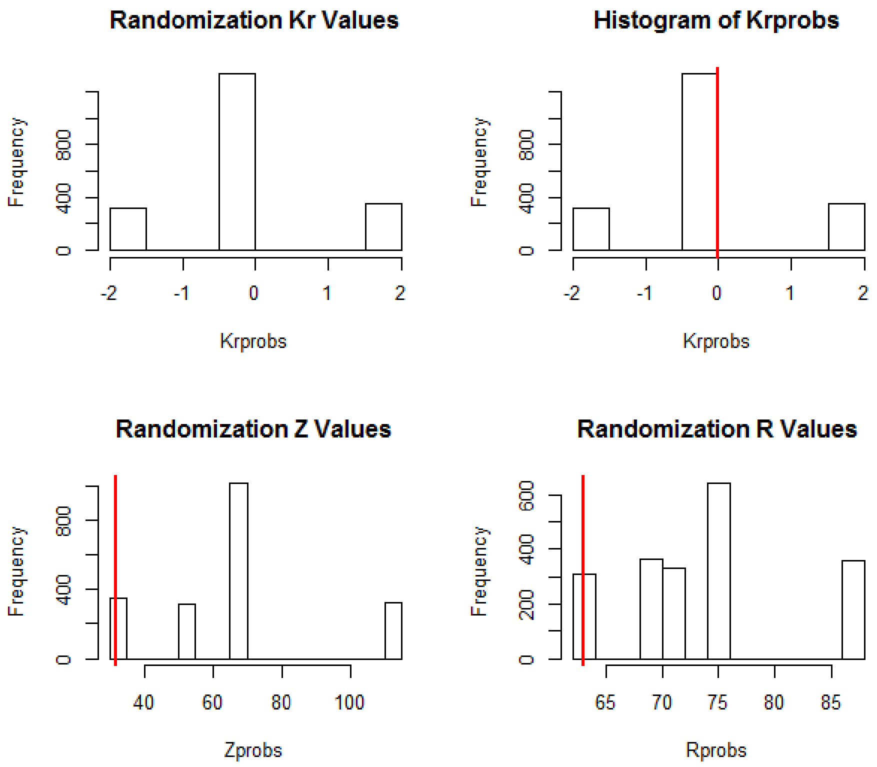
Female Spider Monkey Hierarchy Reciprocity of Food Recieved and Rank



Female Spider Monkey Hierarchy Reciprocity between Food Shared and Rank



Female Spider Monkey Hierarchy Reciprocity of Shared Food

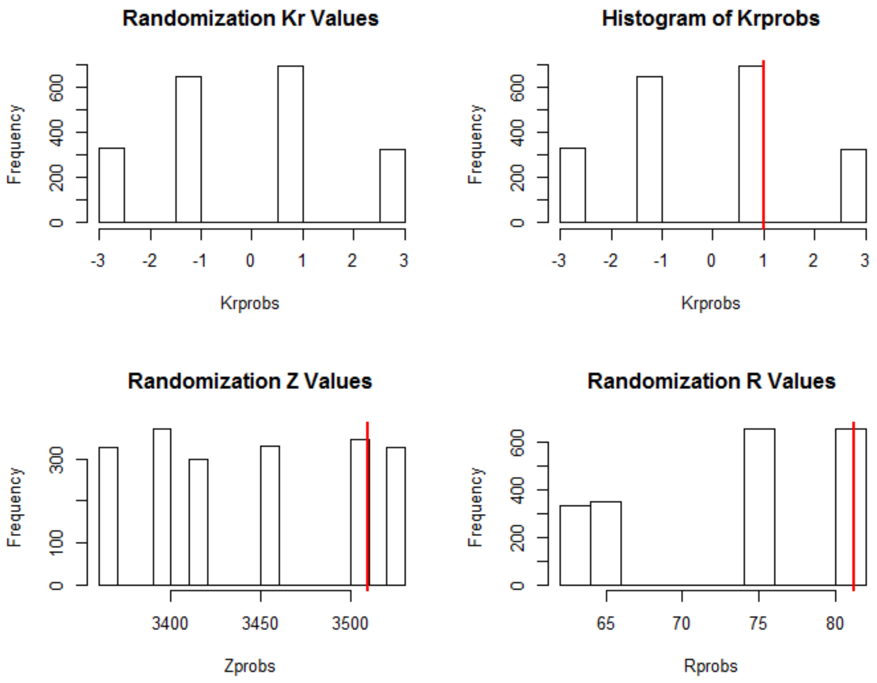

Randomization Kr Values

Histogram of Krprobs

Randomization Z Values

Randomization R Values

Female Spider Monkey Hierarchy Reciprocity of Food Shared and Sleep

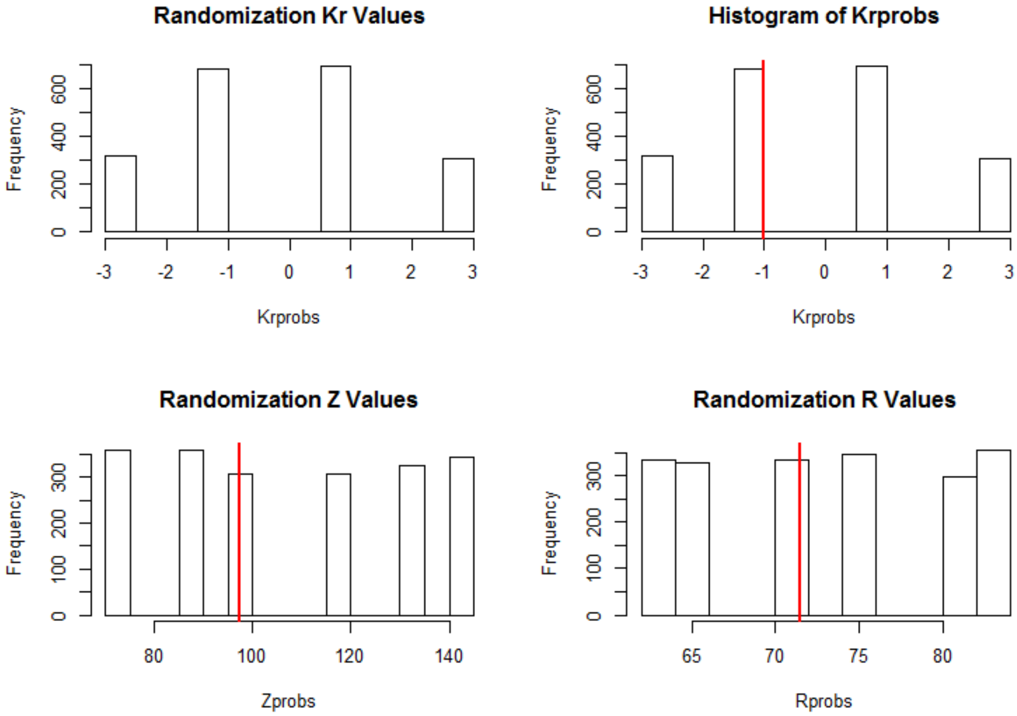

Randomization Kr Values

Histogram of Krprobs

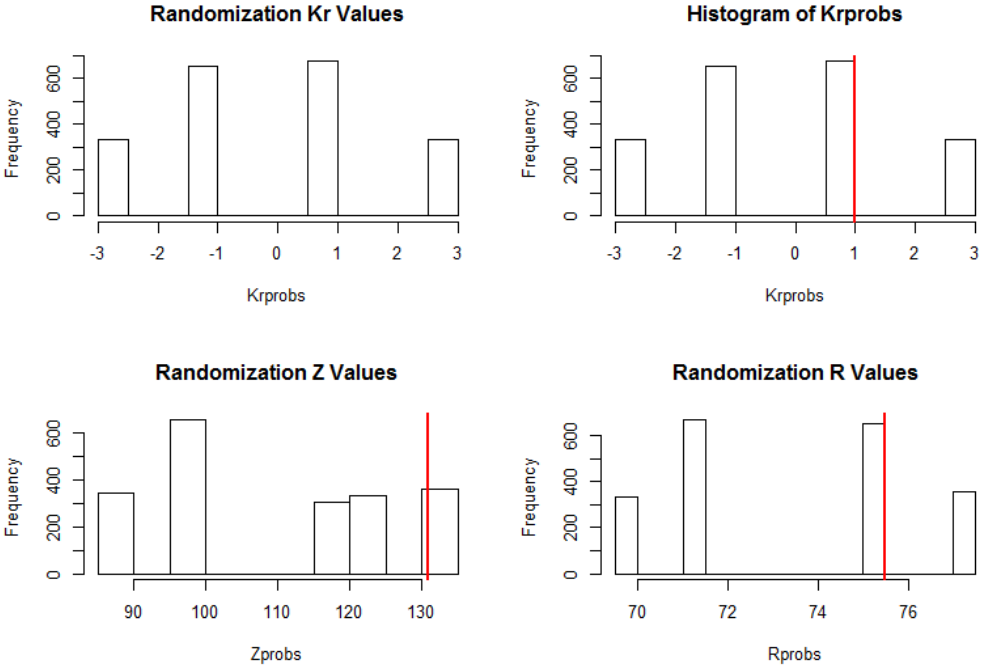
Randomization Z Values

Randomization R Values

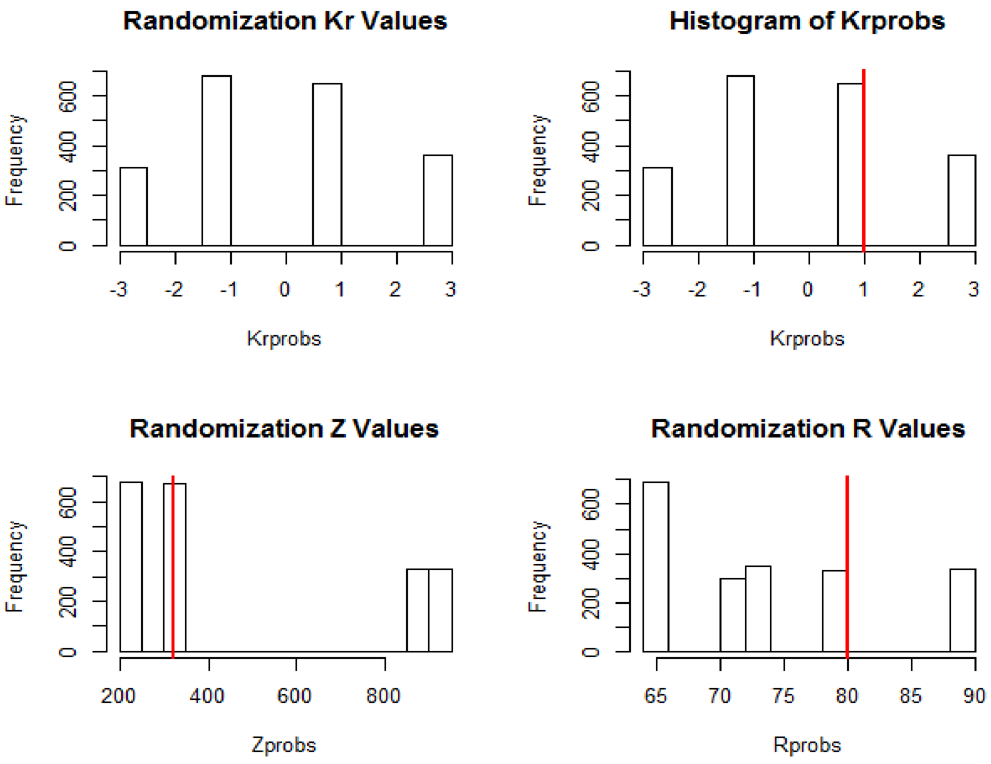
Female Spider Monkey Hierarchy Reciprocity of Grooming Received and Rank



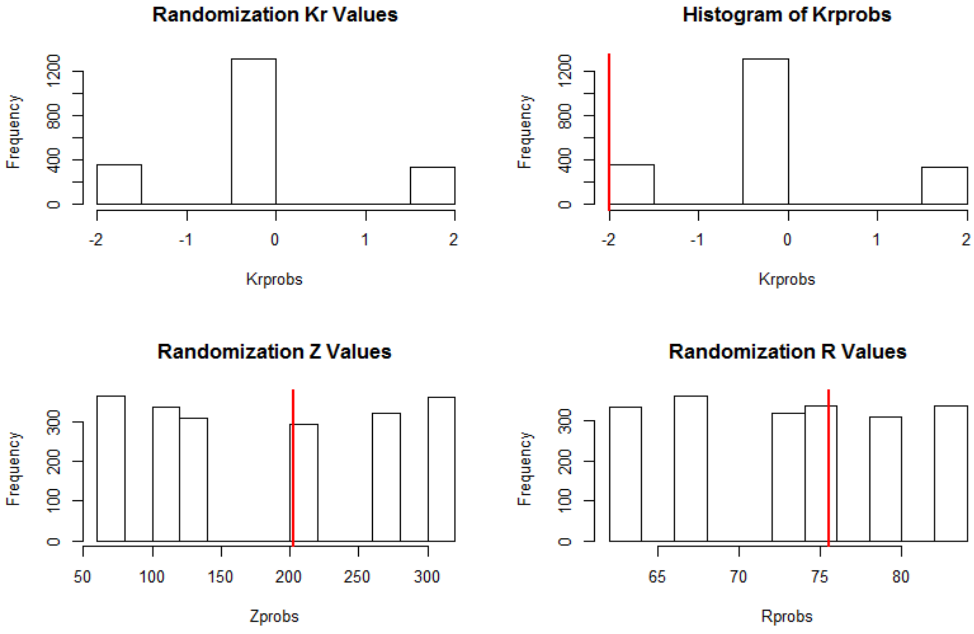
Female Spider Monkey Hierarchy Reciprocity of Grooming Given and Rank



Female Spider Monkey Hierarchy Reciprocity of Grooming



Female Spider Monkey Hierarchy Reciprocity of Grooming given and Food Received



Female Spider Monkey Hierarchy Reciprocity of Grooming Given and Sleep