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## Assessment of Behavior and Social Dynamics in a Newly-Forming Group of Captive Western Lowland Gorillas

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May, 2016

To the Dean of the Graduate School:

We are submitting a thesis written by Sarah Huskisson entitled "Assessment of Behavior and Social Dynamics in a Newly-Forming Group of Captive Western Lowland Gorillas (*Gorilla gorilla gorilla*)."

We recommend acceptance in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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**ASSESSMENT OF BEHAVIOR AND SOCIAL DYNAMICS IN A NEWLY-  
FORMING GROUP OF CAPTIVE WESTERN LOWLAND GORILLAS  
(*GORILLA GORILLA GORILLA*)**

A Thesis

Presented to the Faculty

of the

College of Arts and Sciences

In Partial Fulfillment

of the

Requirements for the Degree

of

Master of Science

In the

Department of Biology

May, 2016

By

Sarah Murphey Huskisson

## ABSTRACT

This study presents behavioral data of a recently-formed western lowland gorilla (*Gorilla gorilla gorilla*) group at Riverbanks Zoo and Garden in Columbia, South Carolina, from the initial stages of group formation through the first several months after introduction. The group consists of a male (19 years), two half-sisters (both 10 years), and an unrelated female (20 years). I collected 15-minute focal animal samples for three hours twice a week in two observation blocks, the first lasting from 7/17/15 to 9/11/15, and the second lasting from 10/30/15 to 1/3/16. A total of 99.25 observation hours were collected. It was predicted that the frequency of affiliative behaviors would increase over time, with more affiliative interactions between related females. Also, it was hypothesized that agonism would decrease over time. Overall, the mean rates of affiliative behaviors did increase between the two observation blocks ( $r_s=0.208$ ,  $p=0.002$ , Wilcoxon Signed-Rank test); agonistic behaviors decreased ( $r_s=-0.185$ ,  $p=0.005$ , Wilcoxon Signed-Rank test). Dyadic rates of affiliation differed significantly ( $Q=39.401$ ,  $p<0.001$ , Friedman test). In male-female dyads, the mean rates of affiliation were significantly different ( $Q=30.537$ ,  $p<0.001$ , Friedman test), whereas they were not in female-female dyads ( $Q=1.288$ ,  $p=0.525$ , Friedman test). Dyadic mean rates of agonism showed no significant difference ( $Q=7.144$ ,  $p=0.210$ , Friedman test).

It was also predicted that a dominance hierarchy would result among the females, with the unrelated female being the lowest-ranking due to the already strong bonds shared by the half-sisters. Evaluation of female hierarchies showed there was no strong relationship among the females' resulting ranks in approach-withdrawal ( $r=0.991$ ,  $p=0.083$ ) or grooming interactions ( $r=0.893$ ,  $p=0.297$ ). The results of this study show that the group-wide and intrasex relationships mirror those seen in wild populations and other captive groups, particularly in regard to the lack of social dominance. It appears that the members of newly-formed group adjusted well and will thrive in their new surroundings. Furthermore, these findings may help animal caretakers more effectively manage family groups and continue to ensure a high quality of life for captive gorillas.

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# INTRODUCTION

Highly social animals like gorillas exhibit a large behavioral repertoire, and thus extremely complex societies. Such animals interact for a variety of reasons and their patterns of interactions can both build and break relationships with members of their social group. Repeated, measurable patterns of interactions can elucidate much about an animal's status in the group as well as whether its approach toward others changes with time (Hinde, 1976).

I studied a captive group of four newly-introduced western lowland gorillas at Riverbanks Zoo & Garden in Columbia, South Carolina, from July 17, 2015 to January 3, 2016 in an effort to better understand captive western lowland gorilla social dynamics. The four subjects of this study were brought together based on breeding recommendations from the Gorilla Species Survival Plan and the Association of Zoos and Aquariums. With the exception of two half-sisters, all individuals were new to their surroundings and to each other. This study allowed a highly informative glimpse into the interactions of a newly-forming family group. Group formation is difficult to observe in the wild, especially with western lowland gorillas, which are notoriously hard to habituate (Parnell, 2002). Furthermore, it is rare that wild gorillas' individual backgrounds are known. The fact that the study subjects are habituated and their histories are known makes for an enlightening evaluation of gorilla behavior that can expand current knowledge. The information gleaned from this project could also help zoo staff to better facilitate other groups' formations in the future.

## **Ethological Studies**

Ethology, according to Tinbergen (1963), is the biological study of behavior. This biological perspective is distinctive because it encompasses the relationship between extrinsic ecological factors and internal physiological or molecular processes.

Two of the fundamental tools of ethology are observation and description, which, in combination, answer the question of why animals behave as they do. Using these tools, scientists can gain a better understanding of how a particular species, and particular individuals within that species, act on a regular basis. A species' behavioral repertoire represents a unique series of adaptations to its niche. Ethologists argue that each pattern of behavior witnessed in an individual and/or a species has been naturally selected for (Tinbergen, 1963). Tinbergen (1963) identified four central questions in the study of ethology, which provide a more complete comprehension of animal behavior. These questions deal with the proximate and ultimate nature of behaviors and help elucidate the mechanisms behind the production of a behavior, the development of a behavior in an individual over its lifetime, the behavior's particular use to an organism, and the evolutionary history of a behavior (Tinbergen, 1963).

Ethological studies can be utilized for a variety of purposes. Perhaps most importantly, information gained from behavioral studies helps scientists implement effective conservation strategies (Sutherland, 1998). Sutherland (1998) suggests several possible applications. Small populations are at a higher risk of

extinction, and thus individuals must be able to identify reproductive behaviors and ritualized mating behaviors of their own species in order to successfully breed. Additionally, hybridization resulting from a species' inability to distinguish mates of a different species can be problematic. In such cases, understanding animal behavior can help scientists ensure that the individuals mate with members of their own species and persist in the wild. Furthermore, behavioral alterations might remedy problems between populations. Sutherland (1998) describes cases where predator species have been introduced to an area. Behavioral modifications to the predator or to the prey species may be more effective than removing the predator species entirely (Sutherland, 1998). For instance, rufous hare-wallabies (*Lagocherstes hirsutus*) were squirted with water each time they saw a stuffed version of a natural predator. That association helped them later avoid these predators in their natural habitats (McLean *et al.*, 1994; Sutherland, 1998).

Behavioral manipulation is vital in zoos, where breeding attempts may fail due to inevitable behavioral changes as a result of living in captivity. Generally, zoos seek to remedy this through the use of naturalistic habitats and environmental enrichment (Hosey, 2005; Rooney and Sleeman, 1998; Sutherland, 1998). Again, none of these solutions can be fully reached without a complete understanding of a species' behavioral range.

## **Behavior of Captive Animals**

Fully understanding a species' behavioral repertoire can greatly improve the lives of animals in captivity. Within the last 40 years, zoos have embraced their roles as institutions of conservation, education, and research. Caring for exotic and endangered species encompasses several objectives, among which are the promotion of species-typical behaviors and preparing for reintroduction to natural habitats where possible (Forthman and Ogden, 1992). Species-typical behaviors may be absent or altered in captive animals. Captivity in and of itself is conducive for the development of abnormal behaviors, due to an animal's lack of control over its own daily schedule (particularly with feeding), space restrictions, and visitor proximity (Hosey, 2005). Zoo personnel work diligently to create naturalistic habitats and provide their animals with environmental enrichment in order to encourage healthy behaviors within their collections, which are needed for successful reproduction and possible reintroduction to the wild. In order for these to occur successfully, the full range of an animal's behaviors must be shown while in captivity (Forthman and Ogden, 1992; Rooney and Sleeman, 1998).

With regard to habitat design, the physical features of captive enclosures must have a positive effect on several aspects of an animal's behavior. Habitats are created to mirror that species' habitat in the wild and to include plenty of biologically relevant features. Environmental enrichment is a key component; it can be used to encourage more natural feeding behaviors, social interaction, cognitive activity, etc. The implementation of proper enrichment for a given

species can vastly improve its quality of life in captivity. Zoo keepers and enclosure designers must also eliminate harmful elements from the animals' areas, like disease-carrying pests and interference from the public (Forthman and Ogden, 1992; Rooney and Sleeman, 1998).

Beyond habitat design and environmental enrichment, several other factors can contribute to the overall well-being of captive animals. Healthy, high-energy diets and frequent feedings keep animals functioning at an optimal level. Giving animals the ability to move freely about their enclosure or shifting them to new areas of the habitat on a regular basis is both physically and mentally stimulating. Similarly, organized training sessions with appropriate positive reinforcement meet the same goals. Training by operant conditioning strengthens important husbandry behaviors that are used to improve daily interaction with keepers and for veterinary examinations. Reinforcing learned behaviors on a daily basis serves to improve physical health as well as psychological welfare (Forthman and Ogden, 1992).

Housing animals in a species-appropriate group including suitable sex ratios also encourages species-typical behaviors. For instance, polygynous species should be kept in groups with several females per male, as opposed to groups having an even sex ratio or more males than females (Forthman and Ogden, 1992). Furthermore, social animals should be housed with other members of their species. In the past, zoos kept some animals, even highly social apes, in isolation. This was the case for Willie B., the well-known Zoo Atlanta gorilla, who was

wild-caught and spent 27 years living alone. Once the importance of a social life was fully understood, zoo staff created a naturalistic habitat and, in 1988, introduced him to a group that he joined quite successfully (Forthman and Ogden, 1992).

The controlled settings in which captive animals live give researchers excellent opportunities to learn more about species and how they interact with their surroundings, providing an easier time of doing so than might be encountered in the wild. Findings from zoo studies can help the study's subjects and fellow members of their species in captivity. In the long term, the results of behavioral studies can be applied to improve conservation initiatives and potentially resolve long-standing issues (Forthman and Ogden, 1992). This is the case for Golden lion tamarins (*Leontopithecus rosalia*), or GLTs. South American GLTs are endangered and have been a species of concern for several years now. Through the efforts of many scientists and zoos worldwide, GLTs have been successfully reintroduced into Brazilian forests, providing much needed genetic diversity to sustain the population (Stoinski *et al.*, 2003).

### **Social Behavior and Organization**

Communication is absolutely necessary within social groups, as it outlines social structure, conveys information to others, and coordinates group activity. In group-dwelling animals, social behaviors are selected for and evolve because they present some significant benefit to the individuals in the group, usually at the

genetic level. Three benefits of social behavior have been suggested: first, it may increase the positive aspects of living in a group (e.g. protection against predators). Second, being social is predicted to increase immune resistance to disease and parasites. Lastly, social behavior increases an individual's competitive ability and access to mates (Alexander, 1974).

Behaviors that arise to fulfill one function can evolve in social groups to fulfill another in addition to their initial purpose. For example, grooming behavior in primates reduces ectoparasite loads but also provides necessary social cues to others that reinforce relationships (Alexander, 1974). Such instances of "multitasking" behaviors undeniably make some social groups highly complex. The complexity of social groups can be linked to increased brain size due to an enlarged neocortical area, which is necessary for intricate social interaction and manipulation (Byrne and Bates, 2007). Large social groups have several advantages, but they also carry disadvantages, such as resource competition (Byrne and Bates, 2007).

To fully understand social organization in any group of animals, dyadic interactions must be considered in great detail. According to Hinde (1976), relationships are the sum of interactions between two individuals. Since behaviors and interactions can be deemed affiliative or agonistic based on context, descriptions of the content, quality, pattern, and frequency of the interactions between two individuals must be noted (Hinde, 1976). The quality of interactions, Hinde argues, can be more important than the behaviors that were actually



performed (1976). The term "quality" can involve the intensity with which a behavior was performed or whether a given behavior resulted in some consequence for the actor or recipient.

Relationships are typically characterized by either a pattern, as in parent-infant relationships, by the unique idiosyncrasies of the individuals in the dyad, or by the effect an interaction has on either individual in the dyad. Interactions can be influenced by a multitude of factors including genetic relatedness or an individual's past history interacting with the other member of the dyad (Hinde, 1976). That being said, being more familiar with each other does not necessarily ensure a stable relationship. Relationships are considered stable not by a constant pattern of interactions but by smooth changes in shared behaviors over time (Hinde, 1976). Studying the patterning of relationships within a group can help ethologists elucidate group social structure (Hinde, 1976).

### **Affiliative and Agonistic Behaviors**

While Sir Solly Zuckerman, a pioneer of primate biology, first argued that sex was the key factor holding primate societies together, the broader realm of affiliation among members of a social group holds far greater importance. Affiliative behaviors are overall positive behaviors that improve an individual's interactions with others in its social group, which can serve to increase that individual's health, reproductive fitness, and mental well-being (Pelligrini, 2008).

Anatomical studies have documented physical components in mammals that promote the ability to form important social bonds. Primates notably exhibit well-developed and well-connected areas of the brain that enhance affiliative interactions within a social group. The most critical regions of the brain associated with the maintenance of social ties are part of the limbic system and include the orbital-frontal cortex, temporal pole cortex, and the amygdala. The orbital-frontal cortex is predominantly involved in decision-making and the expectation of the consequences of those decisions (Kringelbach, 2005). The temporal pole cortex is responsible for memories, which are important for remembering important aspects of life such as friends, enemies, predators, and food sources. This part of the brain can be modulated by the amygdala, the area of the brain accountable for emotional response, as well as the two aforementioned functions (Olson *et al.*, 2007).

Agonistic behaviors are generally negative behaviors that are associated with aggression toward or avoidance of another individual, either a fellow group member or an outsider. Agonism comes about from a variety of stimuli, virtually all of which are perceived threats to some aspect of an individual's well-being. Resource competition is at the root of agonism (Koenig *et al.*, 2004). Additionally, rates of agonism can be influenced by hormonal activity (Adkins-Regan, 2005). Hormones can communicate much from one animal to another, particularly about reproduction. Some hormones like estrogen can encourage affiliative interactions between two individuals in the form of sexual behavior,

such as a successful solicitation and response. Other hormones like testosterone may result in agonistic interactions such as in the case of two breeding males competing to mate with a female. Hormonal activity could potentially increase the agonistic response seen in competing individuals (Brockman *et al.*, 1998).

### **Dominance and Social Status**

In cohesive social groups, not all members are of the same social status. Dominance hierarchies may result when members of a social group differ in competitive ability. That is, some are more able than others to acquire a variety of resources when others are present (Hawley, 1999). Understandably, resource competition may culminate in physical altercations, and as a result, social animals have evolved many ways of mitigating conflict through reciprocation, cooperation, and alliance formation. Social structure stratified by differing levels of dominance represents the social asymmetry seen in some large groups (Hawley, 1999).

Dominance hierarchies based on agonism are quite common (Hinde, 1976). Aggression toward a competitor can ensure that a high-status individual maintains its access to food, reproduction, and other resources as well as keeps its position of leadership, if applicable. Typically, animals of high rank alter their agonistic approach according to a competitor's rank, presumably in order to exert as little energy as possible to win (Leonard, 1979).

Dominance relationships are also illustrated by affiliative interactions directed toward those of higher rank. Grooming is one such behavior, and is perhaps the most extensively-studied social behavior in regard to dominance (Schino, 2001). Primates have been suggested to garner a higher rank or greater tolerance from high-ranking members of their group in exchange for affiliative behaviors like grooming (Schino and Aureli, 2008). It has been observed that primates show a greater "attraction" to those of higher rank when searching for a grooming partner (Schino, 2001). For instance, grooming bouts in chimpanzee communities and some other primates have been observed to be notably longer when the recipient is of a higher status than the groomer (Hinde, 1976). Moreover, large dominance hierarchies are asymmetric in terms of reciprocity, whereas it is much easier to reciprocate grooming or another altruistic action with fewer individuals in a group. The magnitude of differences in power between adjacently-ranked individuals is referred to as steepness. Generally, steepness of hierarchy is most often seen in cases where resource competition is stiff (Schino and Aureli, 2008). Subordinate individuals are more likely to avoid aggressive conflicts and reduce their risk of injury by grooming a higher-ranked individual. This increases subordinates' overall health and allows them to remain a part of the social group. Furthermore, subordinates are not likely to be overthrown by another individual vying for their position (Schino and Aureli, 2008; Schino, 2001).

## **Rank and Reproduction**

At least in the case of males, rank often directly correlates with the ability to acquire mates (Cowlshaw and Dunbar, 1991). The simple fact that lower-ranking or subadult males cannot compete with highly-ranked males due to their social inferiority confers a more successful reproductive rate to those of higher rank (Cowlshaw and Dunbar, 1991). Additionally, the larger the social group, the more likely it is that males of similar resource-holding potential will be able to consistently compete for greater access to females (Cowlshaw and Dunbar, 1991). All of these relationships hold true in most primate species. Specifically in non-seasonal breeders, it is suggested that males of high rank will have an easier time monopolizing more females in estrus, since their cycles vary; that is, high-ranking males will have more chances to mate with more females because breeding is possible at any time (Cowlshaw and Dunbar, 1991). This can serve to reinforce the status of high-ranking males.

## **Societies Based on Female Transfer**

In some cases, individuals may need to leave their natal groups in order to reproduce without the risk of inbreeding. A species' traditional mode of movement can be characterized by male transfer, female transfer, or the transfer of both sexes. The western lowland gorilla is a female transfer species. This particular mode of dispersal can also be found in a few mammalian societies and is quite common in other primate species (Clutton-Brock, 1989; Moore, 1984).

Female transfer-based societies may actually be more advantageous for females. By leaving her natal group, and possibly transferring secondarily to another group later in life, a female might encounter more reproductive opportunities, potentially producing more offspring during her lifetime (Clutton-Brock, 1989).

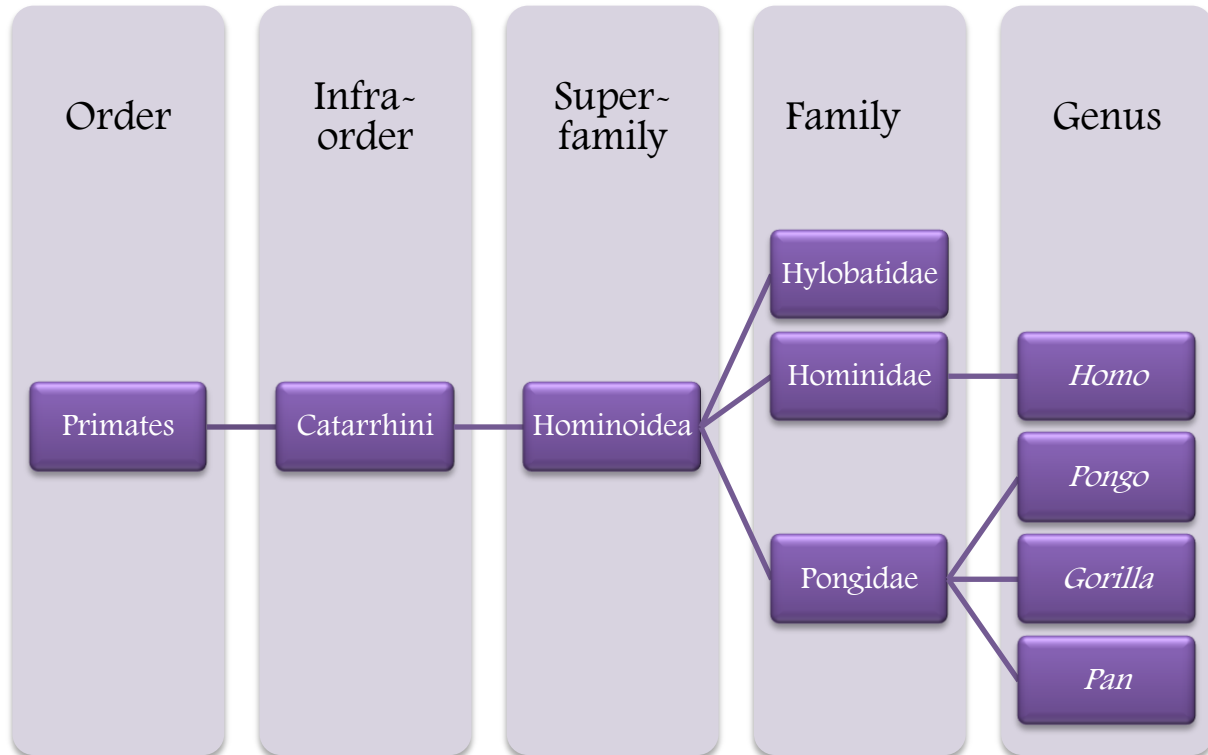
Females must be careful when deciding to secondarily transfer (Stokes et al, 2003). Those female who might already have offspring from one group might put them at risk of predation when moving to another group. In addition, if a female leaves a group that includes several of her female family members, she may lose support in contests of dominance and aggression in her new group (Harcourt and Stewart, 1987; Scott and Lockard, 2007).

### **Study Species: Western Lowland Gorilla**

The study presented here investigates the behaviors, social interactions, and female social status in a newly-formed western lowland gorilla family. The western lowland gorilla is one of Africa's charismatic and highly threatened ape species. Like most primate species, western lowland gorillas are extremely social animals and spend most of their time in groups (Stokes *et al.*, 2003). In the following sections, I will delineate the western lowland gorilla's phylogeny, ecology, life history, and social organization.

## Phylogeny

Western lowland gorillas are members of the order Primates, which consists of 13 families and 233 species. Western lowland gorillas, along with other members of the genera *Gorilla*, *Pan*, and *Pongo*, join humans in the superfamily Hominoidea (Figure 1a) (Harcourt and Stewart, 2007).



**Figure 1a. Phylogeny of Apes. Phylogeny of *Gorilla gorilla gorilla* from order Primates to genus *Gorilla* (Based on information from Groves, 2005; Oates *et al.*, 2008; Walsh *et al.*, 2008).**

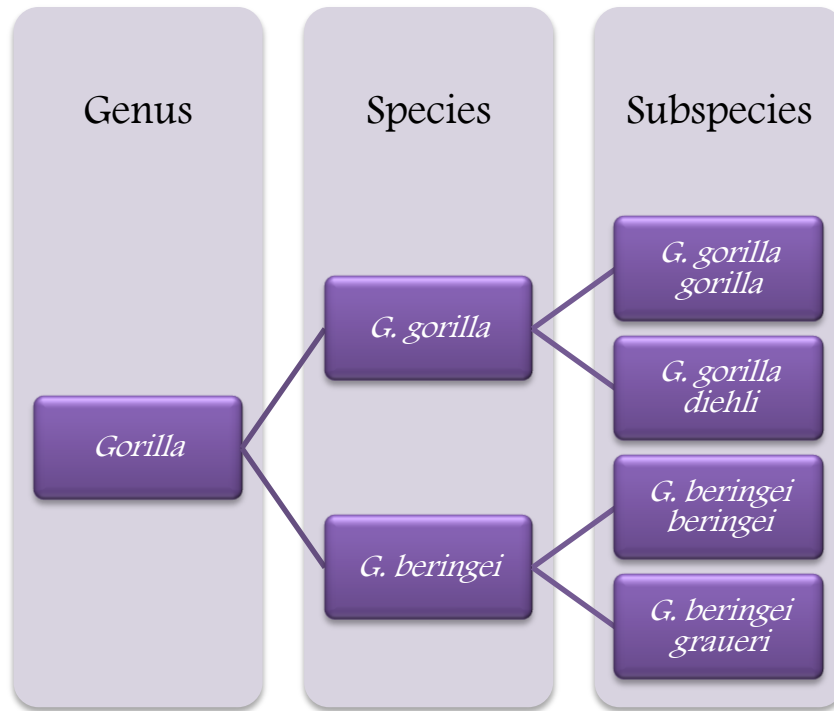
Modern apes diverged from Old World monkeys in the Miocene, approximately 25 million years ago. Around 18 million years ago, the great apes diverged from the lesser apes, which include gibbons and siamangs. Orangutans (*Pongo*) were the first great ape to diverge, which occurred roughly 14 million

years ago. The genus *Gorilla* arose much later, approximately 7 million years ago. Humans diverged from chimpanzees (*Pan*) around 7-8 million years ago (Cachel, 2006).

There is close kinship between *Homo* and the African apes. After chimpanzees, which share approximately 98.8 percent of their DNA with that of humans, gorillas are the closest hominoid relative to modern humans. There is only about a 1.6 percent difference between gorilla and human gene sequences (Cachel, 2006).

Gorilla taxonomy has been a subject of great debate, but genetic analysis has accurately determined the number of species within the genus. Since 2001, it has been accepted that *Gorilla* consists of two distinct species, each of which has two subspecies. *Gorilla gorilla* denotes western gorillas, which include the western lowland gorillas (*G. gorilla gorilla*) and Cross River gorilla (*G. gorilla diehli*). Eastern gorillas, *Gorilla beringei*, are divided between eastern lowland gorillas (or Grauer's gorillas) (*G. beringei graueri*) and the mountain gorilla (*G. beringei beringei*) (Figure 1b) (Groves, 2002; Groves, 2005; Oates *et al.*, 2008; Walsh *et al.*, 2008).

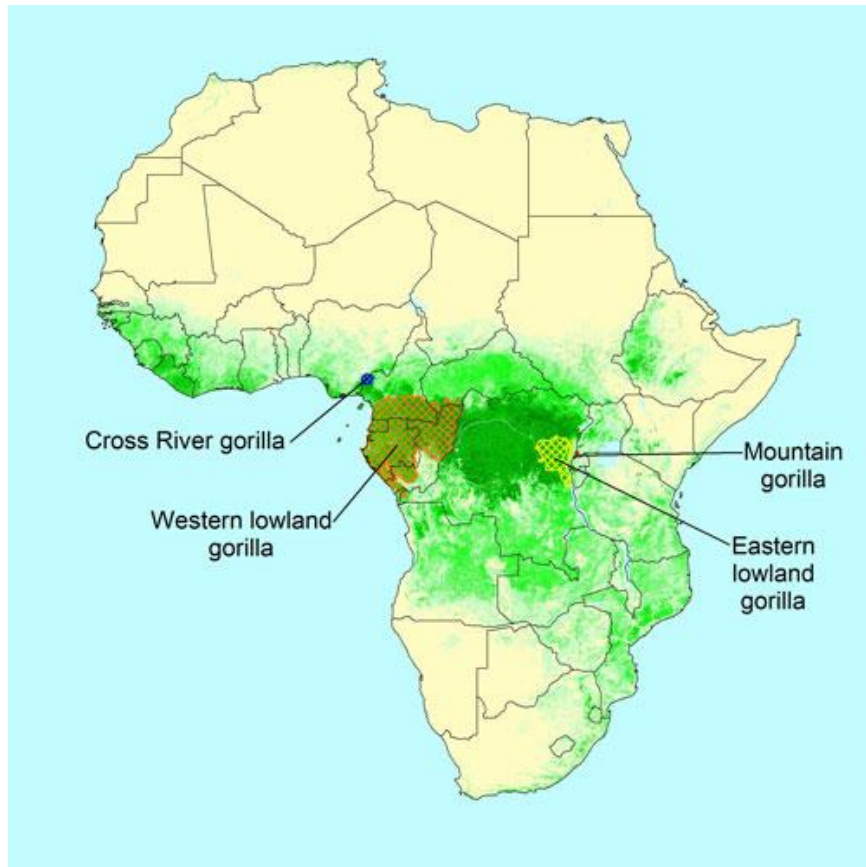




**Figure 1b. Phylogeny of Genus *Gorilla*. (Based on information from Groves, 2005; Oates *et al.*, 2008; Walsh *et al.*, 2008).**

### **Western Lowland Gorilla Ecology, Life History, and Social Organization**

The western lowland gorilla is endemic to central Africa and is found in the countries of Angola, Cameroon, Central African Republic, Republic of the Congo, Democratic Republic of Congo, Equatorial Guinea and Gabon (Figure 2) (Harcourt and Stewart, 2007; Robbins *et al.*, 2004). Of all gorilla subspecies, it is the most numerous (Doran and McNeilage, 1998; Walsh *et al.*, 2008).



**Figure 2. Distribution of Gorilla Subspecies. The range of the western lowland gorilla (*Gorilla gorilla gorilla*) is indicated by orange cross-hatching (Map by Richard Bergl (2008), based on information from Bergl and Vigilant, 2007).**

All gorillas have a unique set of adaptations that allow them to thrive in their densely forested environments. One of these adaptations is their thick hair, which serves to protect their skin from biting, and potentially disease-carrying, insects. In fact, the origin of the term "gorilla" is directly related to hair. Around 2,500 years ago, Hanno the Navigator, a Carthaginian explorer, encountered what are believed to have been wild gorillas in western Africa. The local people called the apes "gorillae," which roughly translates to "hairy person" (Groves, 2002).

Gorillas are predominately herbivorous, consuming mostly leafy green vegetation and fruit, which are abundant in central Africa (Harcourt and Stewart, 2007; Rothman *et al.*, 2006). Western lowland gorillas consumes herbaceous vegetation from both terrestrial and aquatic areas, the latter being acquired during gorillas' occasional swamp-wading endeavors (Doran and McNeilage, 1998).

Fruit comprises about 60 percent of a gorilla's diet, but the amount and varieties of fruits they consume vary with seasonal availability (Rothman *et al.*, 2006). However, western lowland gorillas incorporate far more fruit into their diets than do the other subspecies of gorillas, especially mountain gorillas (Doran and McNeilage, 1998). At western lowland gorillas' living sites, there is an average of 90 different species of fruit, some of which are available year-round. Fruit provides a marginal amount of proteins and fat, both of which are hard to come by in herbaceous vegetation. When fruit is scarce, gorillas often resort to consuming bark, decomposing leaves, and insects in order to obtain their daily allotment of nutrients and calories (Rothman *et al.*, 2006).

In a normal western lowland gorilla diet, nutrients are sparse. Gorillas must eat constantly in order to supply their bodies with adequate energy. These animals have a large colon and cecum, which are adept at extracting nutrients from typically nutrient-poor food sources. Because western lowland gorillas are large, they can cope with eating a great amount of low-nutrient foods (Harcourt and Stewart, 2007). Plentiful intestinal microbes are capable of breaking down cellulose for further nutrient extraction (Bittar *et al.*, 2014). To accommodate the

large percentage of nutrient-poor foods they consume, gorillas normally conserve their energy through rest. On a typical day, gorillas will rest after their morning foraging, doing so for about 33 percent of their day. They also sleep for 13 hours a night, similar to the rest patterns of the other great apes (Harcourt and Stewart, 2007) .

Western lowland gorilla locomotor behavior is shared with all African apes. Gorillas move predominantly by knuckle-walking, which is a quadrupedal mode of locomotion where the fingers are slightly curved in order for the animal's weight to be distributed on the ground through the knuckles. Gorillas can move bipedally for short distances in cases of defense, display, or when carrying food (Richmond *et al.*, 2001).

Western lowland gorillas have a high degree of sexual dimorphism, with fully mature adult males (called silverbacks due to the appearance of silver hair as a result of changing testosterone levels) being about twice the size of adult females. Silverbacks can reach between 1.5-2 meters in height and weigh 130-270 kilograms. Females, on the other hand, usually only reach about 1.5 meters in height and weigh half as much as males. Even so, both genders of gorillas are the largest of the great apes, which is an asset when it comes to defending themselves and their offspring (Harcourt and Stewart, 2007).

The lifespan of wild western lowland gorillas is generally around 35-40 years; their captive counterparts have been reported to live around 50-60 years (Nowak, 1991). Females reach sexual maturity around eight years of age,

although they usually do not give birth until they are 10 years or older (Harcourt and Stewart, 2007). Typically, males are sexually mature around 14 years of age. Usually one offspring is produced per reproductive event, with gestation lasting around 8.5-9 months. Offspring are usually dependent on maternal care for the first four years of their lives, which is shorter than in either *Pan* or *Pongo* (Robbins *et al.*, 2004).

Both male and female gorilla parents play important parts in their offspring's life. Females play a more direct role in their infants' development, as they are their primary caregivers. Male gorillas support infant rearing indirectly, assisting infants and juveniles through the process of socialization with other group members, intervening in cases of within-group aggression, and thwarting the possibility of infanticide from outside males (Harcourt and Stewart, 2007; Sicotte, 1993). All of these factors help ensure the survival and future success of that offspring (Harcourt and Stewart, 2007).

Gorilla societies are polygynous, consisting of units with a single male, multiple nubile (sexually mature) females, and their offspring. Most groups contain a median of three females, which are unrelated in many cases. Western lowland gorillas often have the fewest number of males in their family groups compared to other subspecies of gorillas, which usually include just one dominant male (the silverback) and subordinate males (Harcourt and Stewart, 2007; Parnell, 2002). In the wild, group size and ranging patterns depend on resource availability (Masi *et al.*, 2009; Parnell, 2002). Gorilla group size can range from roughly 8-9

individuals (adults and offspring), to 30 individuals or more when nutrients are abundant. Western lowland gorillas have been seen to have groups at the lower end of this size range, as compared to other subspecies (Parnell, 2002; Robbins *et al.*, 2004).

Unlike males, female gorillas generally do not spend much time outside of a group, as group living provides the best means of defense from infanticide and predation, as well as increased access to resources. Both males and females benefit from group life, as it provides substantial defense against their major predator, leopards, and in more recent years, humans (Stokes *et al.*, 2003).

### **Female-Female Interactions**

Western lowland gorillas, like the other subspecies, are a female transfer species. Here, females leave their natal groups at sexual maturity in order to avoid inbreeding. Typically, females will transfer to another group alone where they are not related to any of the group members. In my study group, two of the females were paternal kin, while the other female was unrelated and joined the group unaccompanied by a female from her previous group.

While western lowland gorillas are gregarious, the relationships among females in a social group vary. Related females have been observed to spend a great amount of time together in their natal groups. Even half-siblings sired by the same male have an overall stronger relationships than females that have no blood connection (Harcourt and Stewart, 2007).

Field studies have shown evidence of minimal social stratification among female gorillas. Researchers commonly classify such societies as "egalitarian" (de Vries *et al.*, 2006) Groups with little to no hierarchy can usually display a lack of ritualized behaviors commonly associated with rigid dominance hierarchies, as well as live in a habitat with universal resource availability (Robbins *et al.*, 2005; Scott and Lockard, 2006; Stokes, 2004; Watts, 1993). Gorilla groups are more individualistic and somewhat less cohesive compared to societies with a traditional dominance hierarchy (Watts, 1993). Interestingly, female western lowland gorillas display more clearly stratified social structures compared to eastern lowland gorillas and Cross River gorillas (Scott and Lockard, 1999).

From groups studied in the wild, status is often determined by "approach-withdrawal" interactions and seniority (Watts, 1993). Females with more experience or better-developed abilities (are excellent foragers, for example) have been observed to obtain a higher social status than their less-experienced and/or younger counterparts (Harcourt and Stewart, 1987; Robbins *et al.*, 2005). Among wild mountain gorilla populations, the high-status females in the group are generally the ones that have been in the group the longest (Robbins *et al.*, 2005). The most obvious indicator of status is grooming; females of higher status are often seen being groomed by lower-status females (Robbins *et al.*, 2005). That being said, grooming typically does not occur in gorillas as frequently as in other primate species (Harcourt and Stewart, 2007). The most common factors responsible for a change in an individual's status are immigration into and

emigration from a group, which are usually brought about by a female's attempt to avoid inbreeding in her natal group or to increase her chances of reproducing via joining the group of a different silverback (Robbins *et al.*, 2005).

Agonistic interactions play a small role in gorilla society, but are still worth considering when examining social structure (Watts, 1993). With such a naturally low frequency of aggression, determining rank solely based on agonistic interactions provides a largely incomplete picture of females' interactions and loses the context of observed aggression (Watts, 1993). When agonistic interactions do take place, females will respond to an aggressive encounter with aggression rather than submitting to their aggressor in the majority of cases (Watts, 1993).

Although rare, female agonism has been most often observed in cases of food competition, which results from occasional resource scarcity. Agonism as a result of food competition comprises about 66 percent of all conflicts observed among wild female gorillas (Harcourt and Stewart, 2007). With specific regard to western lowland gorillas, increased frugivory gives rise to competition for fruit that is usually patchily dispersed, which results in differentiated social relationships among females (Doran and McNeilage, 1998; Stokes, 2004; Tutin, 1996). In some cases, there is cooperation during food acquisition, which is most often seen among relatives. Family cooperation is often an important factor in being both socially and reproductively successful in the group (Harcourt and



Stewart, 2007). For instance, mothers might help their young offspring gather food.

In captive settings, food resources are never scarce. However, their manner of presentation can result in competition among the individuals living in the same family group. Work by Scott and Lockard (2006) noted that in cases where food or enrichment items were highly desirable and/or distributed in a manner that made them physically defendable, clear social hierarchies resulted. These hierarchies were evident by frequent agonistic gestures and vocalizations from higher-status females directed at subordinate females. As seen in wild populations, the females exercising their right to food were older and had been a part of the group longer than the subordinates (Scott and Lockard, 2006).

In a great many primate groups, post-conflict reconciliation between females is common. Reconciliation reinforces the strong bonds that are necessary in group life. One study of captive western lowland gorillas noted little evidence of reconciliation in female-female quarrels. These results are surprising because western lowland gorilla females spend much more time with other females than with males, and thus strong social bonds are necessary. Moreover, because captive gorillas lack the space that wild populations have, they have a greater need to maintain positive relationships with group mates. It is believed that given a greater number of observations and a larger range of study subjects, captive western lowland gorilla females would, in fact, reconcile (Mallavarapu *et al.*, 2006).

Unlike some other primate communities, social standing in gorilla families is not inherited from mother to daughter because of female transfer. Despite this, gorillas can solicit the help of female relatives in their group, if they are present, in situations where another female exerts power based on her elevated position in the group. In aggressive contests, females of lower rank have the potential to outcompete females of a similar age and higher rank as long as they have support in doing so, which usually entails older individuals protecting younger ones in agonistic encounters. This has been substantiated in wild gorilla populations but due to the overall peaceful nature of female gorilla group life, calling upon the aid of a relative is uncommon. When this does occur, it is most often seen when related females are close in age and/or have not yet left their natal group. Where dominance is concerned, body size is a major determining factor in who "wins" in an aggressive encounter (Harcourt and Stewart, 1987).

Living in a minimally-stratified social group is not only beneficial to females, who experience equal access to resources and few instances of aggression, but also to males. Males benefit because it is not in the best interest of their offspring to have differing qualities of life, and for lower-ranking individuals, lesser access to resources. Female emigration from a group can help promote social equality by mitigating or removing the potential for agonistic interactions in dyads (Watts, 1993).

## **Female-Male Interactions**

If serious conflicts between females do arise, the presence of a dominant silverback will often defuse them (Harcourt and Stewart, 2007; Watts, 1993). The rate of male intervention in female interactions is close to 85 percent (Harcourt and Stewart, 2007). Such intervention allows females to use the silverback as a shield, which can explain why aggressive approaches from another group member usually receive aggressive responses from the silverback (Watts, 1993). When a male intervenes in female-female conflict, females will generally appease him with humming vocalizations and some form of physical touch or embrace (Harcourt and Stewart, 2007; Isbell, 1991). A silverback's intervention appears to encourage females to remain in his group, as it indicates that they and their offspring will be protected from antagonistic group members (Cordoni *et al.*, 2006). Unlike cases of female-female agonism, reconciliation can sometimes be seen in male-female aggression (Cordoni *et al.*, 2006; Mallavarapu *et al.*, 2006). Individuals that peaceably interact with one another on a regular basis are quicker to reconcile after a conflict (Cordoni *et al.*, 2006).

Similarly, captive populations of western lowland gorillas appear to reconcile post-conflict, outside of female-female interactions. Male-female and juvenile-adult conflicts are commonly resolved by proximity. Being close to an individual shows interest, but does not directly engage him or her, curbing the risk of reigniting aggression (Mallavarapu *et al.*, 2006). From observed cases, the

victim and aggressor are equally likely to initiate reconciliation (Mallavarapu *et al.*, 2006).

Sexual behavior is a key aspect of male-female interactions in western lowland gorillas. From observation of wild mountain gorillas, approximately 63 percent of all mating events were initiated by females, both in single- and multi-male groups. It is believed that female choice plays just as important a role in western lowland gorilla society (Harcourt and Stewart, 2007). Females in groups led by a single male have been observed to display sexual behavior at all points in their reproductive cycles, even after conception. This is likely due to intra-sex competition for the same male (Douadi *et al.*, 2007; Stoinski *et al.*, 2009).

Essentially, the idea is that females that engage in post-conception mating would deplete the male of sperm, thereby reducing the chances that another female can conceive. A complementary hypothesis is that this behavior could simply be the result of hormonal changes associated with early pregnancy (Stoinski *et al.*, 2009). A study from Zoo Atlanta noted that in captive, one-male families, nonconceptive mating occurred frequently among the females in the group. Females appeared to compete with one another to mate regardless of their reproductive condition (Stoinski *et al.*, 2009).

Nonconceptive mating, either after a female conceives or while she is cycling, also occurs in multi-male western lowland gorilla groups. In these families, this kind of behavior might cause confused paternity, which reduces the potential for infanticide by males who are not the father of the female's offspring.

In situations like this, harming a female's offspring is detrimental to a silverback in the event that it is his own. Additionally, this confusion could support an increase in male investment in the offspring, regardless of whether or not they are actually his. This has been hypothesized for western lowland gorillas, but has been observed in several other primate species, including mountain gorillas and langurs (Stoinski *et al.*, 2009).

Male western lowland gorillas are also focused on improving their own reproductive success. Once a silverback in single-male group has secured a group of females, he has the best chance of mating frequently, which ensures his reproductive success. Silverbacks are notably more aggressive in their guarding of and mating with females in multi-male groups, which make up about 40 percent of all gorilla social groups (Robbins, 1999). In order to attract females, males will give a series of grand displays or touch the female; both behaviors are usually accompanied by intense bouts of neighing, known as "train grunts" (Watts, 1991). Displays often include aggressive gestures that can illustrate a silverback's strength or prowess, like throwing vegetation, chest beating, and fighting with other males (Sicotte, 2002). Lone silverbacks will actively seek out a group possibly to arouse confrontation in order to replace that group's dominant male (Harcourt and Stewart, 2007; Sicotte, 2002).

In groups including multiple males, mating events can involve sexual coercion by a male. Coercive males are most persistent in their efforts toward females in estrus (Harcourt and Stewart, 2007; Smuts and Smuts, 1993). It has

been noted that less coercive males have a better success rate of mating with females in a group than those who are more aggressive (Harcourt and Stewart, 2007).

### **Group Formation in the Wild**

Gorillas are characterized by regular female transfer into and out of social groups (Stokes *et al.*, 2003; Watts 1990). Although it is known that females transfer to avoid inbreeding and increase her access to resources and reproductive opportunities, it is unclear whether group size plays a role in a female's decision to transfer to another group (Harcourt and Stewart, 2007). When moving to a secondary group, females do not always travel alone. Some eastern lowland gorilla females have been seen to transfer to groups with another female from their natal group. It can be assumed that this possibility exists for western lowland gorillas as well, although the species has been less extensively studied (Yamagiwa and Kahekwa, 2001; Stokes *et al.*, 2003).

Male gorillas can also transfer between groups usually for one of two reasons. An adolescent, sexually immature male (blackback) will sometimes be pushed out of his natal group by the dominant silverback. After leaving, the male will often spend some time in isolation or as part of a bachelor group. If this male finds a group of females without a silverback, he will likely join that group (Douadi *et al.*, 2007). When two groups meet, older males may also be supplanted

by a competing silverback, forcing them out of their group (Harcourt and Stewart, 2007).

Silverbacks do not secondarily transfer to a new group nearly as much as females (Harcourt and Stewart, 2007). In some very rare cases, large groups of western lowland gorillas can split up, allowing maturing males to take command of their own unit. Situations like this have been observed in groups with multiple males that are close in age, with enough females for each male (Harcourt and Stewart, 2007).

Inter-group encounters can result in the highest aggression between males, especially since these meetings provide an opportunity for males to transfer to another group (Harcourt and Stewart, 2007). Under these circumstances, a male from a different group could outcompete the resident group's patriarch and kill his offspring, creating more reproductive opportunities for himself (Harcourt and Stewart 2007; Robbins, 1996; Robbins *et al.*, 2013).

### **Group Formation in Zoos**

Captive groups of western lowland gorillas do not have an opportunity to freely intermingle at any time or move to a secondary group. The inability of gorillas to move between family groups, the smaller shared space, and their constant visibility to visitors might be cause for captive western lowland gorillas to exhibit an increased frequency of agonistic behaviors in their interactions with

one another. Making life comfortable for gorillas can decrease agonism and lead to increased reproductive opportunities for the animals in a group (Hosey, 2005).

Zoos hold the responsibility of designing gorilla family groups. Thanks to the substantial work by scientists, there is a much greater understanding of gorilla behavior and ecology. By creating groups with the appropriate gender ratios, there is an increased likelihood of harmonious interactions among group members (Harcourt and Stewart, 2007; Stoinski *et al.*, 2001). In some cases, there is the potential for unrelated males and females to end up in the same secondary group after being raised together as infants. It is believed that the high degree of familiarity will result in an unsuccessful breeding relationship, so zoo managers must act as "dispersal agents" for captive gorillas in order to foster successful breeding (Watts, 1990; Stoinski *et al.*, 2001).

Institutions accredited by the Association of Zoos and Aquariums and their international counterparts have extensive genetic, behavioral, and medical records of every animal they house (Association of Zoos and Aquariums, 2016). These records are key in artificially constructing family groups. When juveniles reach sexual maturity, zoo staff ensure that those individuals are placed in groups where they do not have genetic relatives with which they can breed (as in the case of the half-sisters observed in this study). Genetic diversity is of paramount importance when considering the formation of western lowland gorilla groups and the preservation of the species.



## Conservation Status

Western lowland gorillas are currently listed as critically endangered by the International Union for the Conservation of Nature (IUCN) (Walsh *et al.*, 2008). Human activity is at the heart of western lowland gorillas' endangerment and recent activity has exacerbated the species' decline (Walsh *et al.*, 2008). The easily-spread Ebola virus has plagued wild gorillas for decades, with an observed mortality rate around 95 percent, reducing the world's gorilla populations by a third (Caillaud *et al.*, 2006; Rizkalla *et al.*, 2007; Robbins *et al.*, 2004; Walsh *et al.*, 2008). In addition, areas of Africa where gorilla populations occur are often mined and bulldozed for commercially valuable minerals and lumber, urbanization, and subsistence agriculture. Cleared land makes gorillas even more accessible to poachers, indirectly abetting the bushmeat trade, illegal export, and other profit-generating businesses (Kasereka *et al.*, 2006; Walsh *et al.*, 2008). The national and international regulations that protect threatened species are not well-enforced, and the lack of enforcement is a major problem for wild gorillas (Gates, 1996).

One strategy for protecting gorillas has been to encourage tourism based on viewing them, but the ecotourism business can be both a detriment and a boon to wild gorillas. It has been noted that wild populations are stable for extended periods of time in areas that receive a high volume of tourists. In a long-term study of Bwindi Impenetrable National Park, a tourism hot spot, gorilla groups were larger overall, had a greater number of immatures in their groups, and signs

of illegal poaching were significantly reduced compared to previous years (Kalpers *et al.*, 2013; McNeilage *et al.*, 2001). The reason for the apparent decrease in poaching can be attributed to constantly-increasing law enforcement and public education. Additionally, tourism can be beneficial for humans along with wildlife. Areas with substantial amounts of tourism can generate jobs for local people while helping them recognize the value of animal life. Conversely, the negative effects of ecotourism could be highly damaging to gorillas. Visitors' violation of a park's proximity rules can result in added stress for the animals, as well as an increased risk for disease transmission. Additionally, habituated gorillas can be more susceptible to poaching, as they become used to constant human presence (Kasereka *et al.*, 2006; Sandbrook and Semple, 2006).

Like all great apes, gorillas have a low reproductive rate and cannot easily compensate for any significant loss in numbers in their populations, making them especially vulnerable to a rapid extinction (Bergl *et al.*, 2008; Kalpers *et al.* 2003). If gorillas continue to be plagued by human activity, it is predicted that all gorilla subspecies will experience an 80 percent decline within the next half a century (Rizkalla *et al.*, 2007; Walsh *et al.*, 2003). The implementation and enforcement of multiple, strong conservation initiatives could be the determining factor in whether Western lowland gorillas will persist in the wild (Kalpers *et al.*, 2003).

## **Study Rationale**

The present study offered a unique chance to study the formation of a gorilla family group in which all members were new to both their surroundings and to one another. The objective of this study was to observe the social dynamics of this group as it formed, including the frequency of affiliative and agonistic behaviors, as well as female-female and male-female interactions. A major goal of this project was to determine if a stratified social organization would develop among the females. Social stratification usually results from intra-sex competition for resources. The individuals in this group receive plenty of water and food in their habitat, so resource competition should be low, if there is any. Harcourt and Stewart have noted that kin typically spend more time together than with unrelated individuals, and kin also help each other in contests of dominance (1987; 2007). Since the new group contained a pair of half-sisters, it was predicted that these females would interact much more frequently with each other and would use each other's support in obtaining a higher social status than that of the unrelated female, despite the fact that she was older.

Furthermore, since related females have characteristically been noted to interact peacefully, the half-sisters were predicted to exhibit a higher frequency of affiliative behaviors and a lower frequency of agonistic behaviors toward each other than to the unrelated female (Harcourt and Stewart, 2007). It was also predicted that frequency of affiliative interactions would increase and that the frequency of agonistic interactions would decrease among the females over time.

A male gorilla in a single-male group is the dominant figure of his group, as he strictly governs the group's activities and the female interactions. When a new silverback takes over a group, he may use aggression and coercive behaviors toward females in order to gain control over the group (Harcourt and Stewart, 2007; Watts, 1993). I hypothesized that the newly-forming group's silverback would act accordingly, where the frequency of affiliative interactions would increase and the frequency of agonistic interactions would decrease over time as he interacted with the females.

I also wanted to investigate if stereotypical behaviors constituted a significant amount of the observed behaviors within the group. Captivity alone can lend itself to an animal adopting uncharacteristic behaviors, but the new environment in which the study subjects found themselves could easily have increased the occurrence of such behaviors (Bennett and Fried, 1990; duBois *et al.*, 1991; Forthman and Ogden, 1992; Hosey, 2005; Lukas, 1999). I hypothesized that the frequency of any witnessed abnormal behaviors would decrease from the first block to the second block.

Captive studies provide excellent opportunities to observe animal behavior in detail. Data gathered from research with captive animals can contribute significantly to the knowledge of particular nuances in a species' behaviors. However, captivity is inherently unnatural and so can influence the types and frequency of behaviors and interactions witnessed. For this reason, captive studies should be, and often are, validated with complementary field work.

Precise knowledge of social behaviors are paramount in effectively managing captive groups of animals. For scientists studying captive animals, ethological studies provide a non-invasive way to assess animals' overall wellbeing without disrupting their daily activities or creating unnecessary stress (Hosey, 2005; Tinbergen, 1963). Behavioral studies also shed light on each individual's personality, which can help animal management personnel to tailor the care that animal receives (Gold and Maple, 1994). Careful long-term observations of the behavior of individuals can assist those responsible for managing socially complex species by allowing them to better detect changes or abnormalities in behavior, evaluate whether these are problematic, and determine if action is required to remedy the situation (Tinbergen, 1963).

Western lowland gorillas have been notoriously hard to habituate and observe in the wild, which is why ethological studies at zoos are so essential to better understand the subspecies (Harcourt and Stewart, 2007; Parnell, 2002). Moreover, there is an absence of data regarding this particular subspecies of gorilla, comparatively speaking. The number of captive and field studies concerning western lowland gorillas have increased in recent years, but in the meantime, an incomplete understanding about one aspect of western lowland gorilla life must be filled in with information from the other three subspecies (Parnell, 2002). This study will add expand existing knowledge on western lowland gorillas with the help of study subjects of known backgrounds. Given the precarious nature of wild western lowland gorilla populations, effective

management techniques are of the highest importance for captive gorillas (Walsh *et al.* 2008). The survival of this species may eventually depend on our being able to reintroduce captive-bred individuals into their natural habitats.

## **MATERIALS AND METHODS**

### **Ethics**

This study was conducted in compliance with regulations of the Association of Zoos and Aquariums, the Gorilla Species Survival Plan (SSP), the Winthrop University Institutional Animal Care and Use Committee, and the animal care protocols established at Riverbanks Zoo and Garden. No invasive sampling techniques were utilized.

### **Study Subjects**

I conducted an ethological study of the newly-forming western lowland gorilla group at Riverbanks Zoo and Garden in Columbia, South Carolina. The study group consisted of four adult western lowland gorillas, three females and one male. In the wild, western lowland gorillas groups contain a median of three females, one silverback, and their offspring, thus the group at Riverbanks Zoo and Garden is quite similar to the structure of wild groups (Harcourt and Stewart, 2007). Groups with appropriate gender ratios aid in the promotion of species-typical interactions among individuals (Stoinski *et al.*, 2001). Each individual was distinguished by unique physical features and differences in size. Details of each individual's weights, ages, and sexes can be found in Table 1.

**Table 1. Gorillas' Demographic Information. Demographic information and weights taken at latest physical examination on 11/29/2015 (Emily Lopez Guertin, Senior Keeper of Gorillas/Small Mammals, personal communication).**

<b>Individual</b>	<b>Sex</b>	<b>Age at Time of Study (years)</b>	<b>Weight (kg)</b>	<b>Zoo Transferred From</b>
<b>Cenzoo</b>	Male	19	161	Birmingham Zoo
<b>Acacia</b>	Female	20	78	North Carolina Zoo
<b>Macy</b>	Female	10	64	Zoo Atlanta
<b>Kazi</b>	Female	10	60	Zoo Atlanta

Each individual was captive born. Cenzoo, the group's silverback male, was born February 2, 1996 at Lincoln Park Zoo in Chicago, Illinois. He arrived at Riverbanks in February 2015. The oldest female, Acacia, came to Riverbanks in March 2015. She was born at the Oklahoma City Zoo on January 14, 1995. The remaining two females, half-sisters Kazi and Macy, arrived in April 2015. They share the same father, Taz, but have different mothers (Kuchi and Kudzoo, respectively), all of whom still reside at Zoo Atlanta. Kazi was born on October 31, 2005 and is unique in that she is part of one of the only sets of gorilla twins in North America. Macy was born on December 12, 2005. The two females were raised in the same family group at Zoo Atlanta.

This group was created at the recommendation of the Gorilla Species Survival Plan and the Association of Zoos and Aquariums. All individuals in this group are sexually mature and reproductively intact. Cenzoo has previously sired one offspring, a male named Bolingo, who resides at Busch Gardens Safari Park in Tampa, Florida. Acacia gave birth in 2013 at the North Carolina Zoo to a male

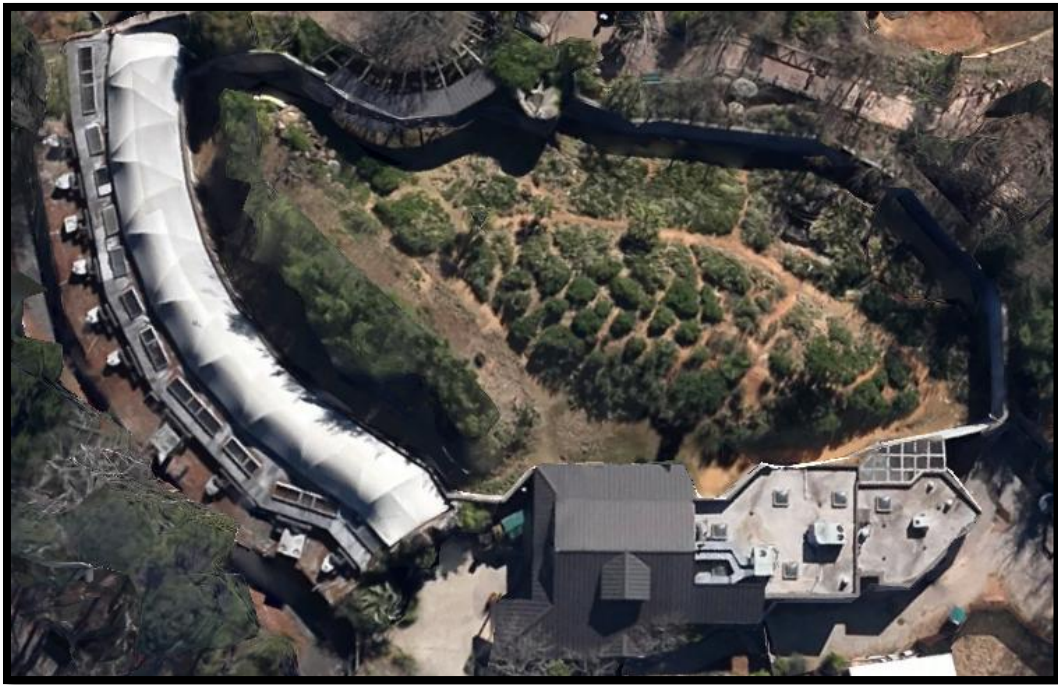


infant. She had a difficult labor and required a Caesarian section to deliver. The pair appeared to be doing well after the birth, but keepers found her baby dead shortly after. Acacia's high-risk delivery makes her no longer recommended by the Gorilla SSP to breed and so she will remain on birth control. However, Acacia has helped raise two other baby gorillas, Bomassa and Apollo, both of whom were born to females living in her group at the North Carolina Zoo (Brian Goleman, Keeper of Gorillas/Small Mammals, and Emily Lopez Guertin, Senior Keeper of Gorillas/Small Mammals, personal communication). Neither of the half-sisters have given birth before, but their medical histories make them excellent candidates to breed. None of the potential breeding partners in the new group had met each other prior to sexual maturity, making this particular group more likely to produce offspring (Stoinski *et al.*, 2001). All the females were kept on contraceptives for the duration of the study.

### **Study Subjects' Housing Conditions**

The captive group was housed in the indoor and outdoor enclosures at Gorilla Base Camp at the zoo. When the gorillas are outdoors, they are separated from visitors by chain link fencing. The outdoor area contained myriad types of shrubs, trees, and bamboo for consumption, shelter, and a visual barrier to the public. Water was available *ad libitum*, from drinking spigots of city water as well as a waterfall in the center of the yard containing water from the neighboring Saluda River.

At two ends of the yard, there are two roofs that provide shade for the gorillas as well as a prime viewing area for the public. One of these roofs is connected to a large indoor viewing room for zoo visitors with a glass window where the majority of one side of the outdoor enclosure can be seen. From this room, part of the sleeping areas can be viewed through a smaller window as well. The other roof is surrounded by cooling misters that are used in the summer months. Figure 3 shows a computer-generated image of the outdoor and indoor (lower right) enclosures created from satellite imagery captured by Google Earth (Google Earth, 2015).



**Figure 3. Study Group's Enclosure. Computer-generated satellite image of the Gorilla Base Camp enclosure at Riverbanks Zoo and Garden, Columbia, SC (34° 0'33.76"N 81° 4'17.56"W) (Google Earth, 2015).**

## **Animals' Daily Routine**

The gorillas' daily schedule included the first of three feedings at 0830. The adult male received vegetables and lettuce and the females got biscuits and green peppers. Everyone received fruit as part of their morning training, which consisted of a review of behaviors they have learned. These behaviors assist staff with conducting veterinary evaluations. For instance, a gorilla might be asked to present a certain body part, like an ear or a foot, in order to have it inspected by a member of veterinary staff. Also, these behaviors help keepers with performing everyday tasks, like shifting gorillas between enclosures, as the gorillas understand some vocal instructions. At 0930, the gorillas were given access to the outdoor enclosure, where they were allowed to move about, interact, and forage as they pleased. After cleaning the enclosure, keepers distributed romaine lettuce, cabbage, turnips, cucumbers, celery, and other green vegetables, as well as enrichment items that included foods like oats, popcorn, and seasonal pumpkins. Between the hours of 0930 and 1700, the gorillas had free access to their 0.6-hectare outdoor enclosure. During this time, the animals were prevented from using their indoor enclosure and sleeping areas during visiting hours. At 1330, the adult male received four to six heads of lettuce as part of his special diet during a public feeding. After the presentation, the females usually had access to whatever was left. At 1630, the group was brought back inside for the third feeding of the day. The male received his remaining allotment of vegetables and lettuce, while

the females were given more biscuits, vegetables, and lettuce. Everyone received fruit once more during their second training session of the day.

### **Behavioral Definitions**

Gorillas are highly social and active animals. As such, they have a behavioral repertoire that covers an array of contexts. For the purposes of collecting behavioral data, I compiled a list of certain behaviors to construct as complete and concise an ethogram for captive gorillas as possible. The definitions of each behavior, presented below, are adapted from the ethograms of Bennett and Fried (1990) and duBois *et al.* (1991), whose studies focused specifically on captive gorillas and whose projects were conducted under the direction of the Gorilla Species Survival Plan. I also utilized the work of Kalan and Rainey (2009), Kuhar *et al.* (2006), Carrasco *et al.* (2009), Stoniski *et al.* (2009), and Sicotte (2002) to categorize behaviors as either agonistic or affiliative in their given contexts.

The animals' behaviors were classified into two main categories, social and nonsocial behaviors. Nonsocial behaviors were performed by the focal individual when it was more than three meters away from conspecifics or there was no interaction with another individual. These behaviors are broadly classified in sub-categories as locomotor, self-directed, and exploratory behavior, and are described in Table 2. Social behaviors occurred within a distance of three meters of other conspecifics and were classified as either agonistic or affiliative (Table

3). Agonistic behaviors were those that always occurred in aggressive situations or in displays, such as those of male dominance. Affiliative behaviors were those that were either pacifying, cooperative, encouraged group cohesion, or were of a sexual nature.

**Table 2. Definitions of Nonsocial Behaviors. Descriptions and abbreviations of nonsocial behaviors Adapted from Bennett and Fried, 1990 and duBois *et al.*, 1991.**

<b>Behavior</b>	<b>Abbreviation</b>	<b>Description</b>
<b>Locomotor</b>		
Walk	WQ/WB	Walk on all fours or hind two legs
quadrupedally/bipedally		
Run	RQ/RB	Run on all fours or hind legs
quadrupedally/bipedally		
Stand quadrupedally/ bipedally	SQ/SB	Stand on all fours or hind legs
Scoot	SC	Quick slide on floor while in seated or laying position
Climb	CL	Climb up or down a structure in enclosure
Sit	S	Sit with legs flat on ground in an upright position
Squat	SU	Squat
Lie	LV/LD/LS	Lie down ventrally/lay dorsally/lay on side
Ventrally/Dorsally/Side		
Swing	SW	Swing on structure in enclosure to move from one place to another
<b>Self-Directed</b>		
Autogroom	AG	Grooming one's self
Masturbate	M	Masturbate
Scratch	SR	Quick scratch of a part of the body, not prolonged examination as in autogrooming
Forage	FO	Actively searching for and consuming food
Drink	DR	Drink from any of the enclosure's water sources
Stereotypical Behaviors	ST	Abnormal behaviors, including head rolling, R/R (regurgitation and reingestion), etc.
Yawn	Y	Fatigued yawn not directed at a particular individual; performed when individual was in relaxed position (sitting, lying down)
Eliminate	EL	Excretion or urination
<b>Exploratory</b>		
Visual Inspection	VI	Visual inspection of object, another individual, or surroundings
Olfactory Inspection	O	Olfactory examination of an object or environment
Gustatory Inspection	G	Examination of an object or surroundings with mouth; independent of foraging
Object Manipulation	OM	Touching/moving object in enclosure; independent of foraging

**Table 3. Definitions of Social Behaviors. Descriptions and abbreviations of social behaviors listed. Adapted from Bennett and Fried, 1990 and duBois *et al.*, 1991.**

<b>Behavior</b>	<b>Abbreviation</b>	<b>Description</b>
<b>Affiliative/Sexual</b>		
Sexual Solicitation	SI	Usually initiated by a female, this display of receptivity is indicated by prolonged staring, arm extension, or head/body jerk
Sitting in Close Proximity	S	Individual sits within 1 meter of another for more than 30 seconds, most common sign of affiliation
Mount	MO	Usually initiated by a male, mounting signals both attempted and successful mating
Grooming	GR	Grooming of another individual
Greet	GT	Greeting another individual as it approaches through a kiss, muzzle-muzzle touch, or embrace
Play	PL	Displayed by a variety of actions, including repeated somersaults, clapping, chuckling, and exaggerated movements
Touch	T	Touching another conspecific in the form of a pat or partial embrace. Brief in duration
Tandem Walk	TW	One individual grabs another around the waist and the pair walk bipedally together
Social Locomotion	SLO	Locomotion other than tandem walking where individuals are in close proximity while in motion. Commonly seen as following other members of the group
<b>Agonistic</b>		
Supplant	SP	One individual takes another's place in the enclosure or food/object in their possession
Threat	TH	Any warning signal directed toward a conspecific, including staring, chest beating, ground slapping, or rigid stance
Attack	AT	Physical violence directed toward a conspecific, typically seen after a threat. Includes hitting, pushing, charging, and biting
Display	D	Male display. Can include throwing vegetation and/or any threatening behavior paired with running and/or sliding. Performed in an aggressive context.

<b>Approach/Withdraw</b>		
Approach	APP	Animal approaches another within three meters
Withdraw	WI	Animal leaves approaching individual and moves outside a three meter range

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Individuals' frequency of approaches (APP) and withdrawals (WI) were recorded as well, and combined with instances of supplanting in the analysis of the females' social status.

### **Data Collection**

This project was conducted using the focal animal sampling techniques as described by Altmann (1974). In focal samples, one individual is observed at a time and all behaviors seen during the observation periods are recorded continuously, over a fixed length of time. I also made use of *ad libitum* sampling to record important affiliative or agonistic behaviors performed by an individual who, at the time of observation, was not the focal animal. Observations began once all individuals were on exhibit as a group and were broken up into two 9-week blocks. The first observation block began on July 17, 2015 and continued until September 11, 2015. The second observation block began October 30, 2015 and continued until January 3, 2016. Dividing sampling into two blocks separated by two months allowed me to compare individuals' behavior during the very first weeks of group formation with their interactions after being together for several months. In total, I recorded 99.25 hours of observations, with 49.75 hours in Block 1 and 49.5 hours in Block 2.



Observations took place during the zoo's normal hours of operation when the animals were on exhibit. Observations were equally divided between morning and afternoon time periods, with morning observations occurring between 0800 and 1130 and afternoon observations taking place between 1330 and 1700. The reason for this was to ensure that if there were differences in behaviors at different times of the day, these were equally likely to be captured in the sample.

In this study, 15-minute focal samples were used for each individual as part of a 60-minute observation session. To minimize travel time and cost, three 60-minute observation sessions were conducted at each visit. Each session was separated by a 10-minute observer rest period. Focal animal sampling was rotated among all individuals using a random number system to determine order of observation in each observation session. In cases where a certain individual could not be seen on exhibit within a 60-minute sampling period, a random number was generated once more to select another individual to observe. Random number selection began again at the beginning of a new hour. The total observation time for each individual over the course of the study is listed in Table 4.

The data recorded for each focal sample included the focal individual's behaviors, the duration of the behaviors, and other specific details about the behaviors (Appendix 1 includes a sample data collection sheet). The context of the behavior was also documented as necessary for actions that could be considered either affiliative or agonistic. For dyadic interactions or interactions with multiple individuals, the actor (who initiated the behavior) and recipient(s) of

the behavior (to whom that behavior was directed) were also noted. While my analysis focused primarily on social behaviors, as they directly pertained to the research questions, the nonsocial behaviors were also recorded to provide context surrounding the focal individual's social behaviors or the actions or reactions of conspecifics.

I recorded each instance of affiliative or agonistic behaviors performed by individuals who were not the focal animal, *ad libitum*, at the time the behavior was seen. It was possible to record *ad libitum* behaviors while still keeping track of the focal individual, due to the small number of individuals in the group.

**Table 4. Focal Animal Sample Minute Breakdown and Totals. Sample observation time (in minutes) for each individual is listed for each observation block .**

	<b>Macy</b>	<b>Kazi</b>	<b>Acacia</b>	<b>Cenzoo</b>	
<b>Block 1</b>	795	735	675	780	
<b>Block 2</b>	735	765	750	720	
<b>Total</b>	<b>1530</b>	<b>1500</b>	<b>1425</b>	<b>1500</b>	<b>5955</b>

### **Data Analysis**

All of the following statistical analyses were carried out using IBM SPSS Statistics, Version 22.

#### *Rates of Affiliative and Agonistic Behaviors and Dyadic Interactions*

Social behaviors were evaluated based in the context in which they were observed and were recorded accordingly as either affiliative or agonistic.

Important social behaviors were counted outside of an individual's focal period if

they were observed. In some cases, social behaviors were directed at multiple individuals in a given instance, like aggressive or dominant displays, and thus were not included in dyadic interactions and were counted just for that individual. Also, some social behaviors (e.g. play, threat) were performed by a lone individual in response to the environment (e.g. visitors in close proximity) and not directed toward another individual in the group. Such behaviors were also left out of dyadic interactions and were counted as affiliative or agonistic just for that individual.

An individual's tallies of agonistic and affiliative behaviors were converted to mean rates per hour for both blocks. Mean rates were compared among individuals and between the two blocks. To better understand the composition of the means of social behaviors, means of each behavior, which were presented in Table 3, were recorded for each individual and compared among group members and between blocks. To test whether the means of each behavior differed between blocks, an Independent Samples Mann-Whitney U test was performed. With regard to differences between individuals, an Independent Samples Kruskal-Wallis test was conducted.

Some behaviors (e.g. play and touch) repeatedly occurred close together during the observation periods. I performed a Spearman's rank correlation to test whether certain behaviors were correlated with one another if they were observed together.

To determine whether the mean rates of affiliative and agonistic behaviors changed in dyadic interactions over the two observation blocks, I used Spearman's rank correlations. Spearman's rank correlations were also used to determine whether the rate of affiliative behaviors were correlated with the rate of agonistic behaviors overall. Additionally, the rates of affiliative and agonistic behaviors over the two observation blocks were further evaluated on the basis of female-female and male-female dyads to determine whether any gender-specific behavioral patterns could be elucidated and account for reported differences.

To test for differences in the mean rates of affiliative and agonistic interactions among all the dyads, I used a Related Samples Friedman Two-Way ANOVA by Ranks. When overall significant differences were found, I conducted a Wilcoxon Signed-Rank test to locate the differences between means. A Bonferroni correction was used to keep the test-wise error at 0.05.

When apparent differences in affiliative behaviors arose, they were further investigated using a Friedman test once more within two dyad types, female-female and male-female. Within each dyad type, differences between mean ranks were evaluated by a Wilcoxon Signed-Rank test, once again using a Bonferroni correction.

### *Determining Female Dominance Hierarchies*

Captivity is conducive for the formation of a stratified social hierarchy due to confined space and easily-defendable food resources (Scott and Lockard, 2006;

Stokes *et al.*, 2004). To analyze female social status, the number of approaches and withdrawals were used. I recorded the approaches of focal animals that resulted in a withdrawal by an individual to elucidate a female dominance hierarchy. If an individual was approached and there was no subsequent withdrawal, the behavior was not included in the analysis of rank. If a focal animal approached an individual and sat within three meters, it was counted as an affiliative behavior.

Social status was determined through the construction of matrices. Regarding approach-withdrawal interactions, I turned the counts of approaches and withdrawals per female into rates per hour for each observation day. To obtain the total rates for each block, I calculated a mean rate per day for each female. The rates were arranged so that the approaching females were on the horizontal axis and the females who withdrew from an approach were on the vertical axis (Tables 6a and 6b). The females, ranked one to three, are arranged so that the highest-ranking female is toward the top of the matrix and the lowest-ranking is toward the bottom. Female dominance matrices were created for each block. I also evaluated approaches and withdrawals involving the silverback to account for his influence on the females' rates of withdrawal outside of the female dominance matrix. Mean rates of withdrawal from the male were compared to mean rates of withdrawal from another female using a Wilcoxon Signed-Rank test.

Grooming was also taken into account regarding a female's rank. The act of grooming is unambiguous, making it a good indicator of affiliation and status among individuals (Henzi and Barrett, 1999). Grooming is less often apparent in female-transfer gorilla groups than in highly stratified, resident-female societies. However, subordinate females still frequently groom to appease their superiors, regardless of living situation (Hemelrijk and Luteijn, 1998). Although a female transfer species, western lowland gorillas still groom, and females who are groomed most often are usually those of elevated social rank.

Bouts of grooming were also recorded in a matrix. Similar to the approach-withdrawal matrix, the groomers were listed on the horizontal axis and the recipients of the grooming were listed on the vertical axis. Females were ranked one to three in the same fashion as the approach-withdrawal matrices. Again, I took the counts of grooming and turned them into rates per hour per day and mean rates per day for each female.

Landau's index of linearity ( $h$ ) was used to determine the rigidity of social stratification. A rigid social hierarchy would yield a linear relationship, whereas a lack of a hierarchy would be nonlinear. The index used to describe linearity ranges from 0 to 1, with 1 being indicative of a perfect linear hierarchy and 0 representing a complete lack of a hierarchy and a nonlinear relationship. Landau's index of linearity ( $h$ ) can be calculated as follows:

$$h = \frac{12}{N^3 - N} \sum_{j=1}^N \left[ V_j - \frac{(N-1)}{2} \right]^2$$

In this equation,  $V_j$  is the number of individuals dominated by  $j$  and  $N$  is the total number of individuals in the group (Landau, 1951).

I also calculated the steepness of the hierarchy obtained from the matrices to better determine the degree to which the females differ from each other in terms of withdrawal and grooming. I used the protocols outlined by de Vries *et al.* (2006), which calls for the use of David's score to find the proportion of "wins and losses" within dyadic interactions. David's score is calculated using the following:

$$DS = w + w_2 - l - l_2$$

Here,  $w$  is the sum of wins and  $l$  is the sum of losses, and  $w_2$  and  $l_2$  are weighted sums of wins and losses in dyads with particular individuals.

Normalized David's scores (*NormDS*) lie between 0 and  $N-1$  and can be used to give a rank to each individual. They are calculated using the following formula:

$$NormDS = \frac{\{DS + MaxDS(N)\}}{N} = \frac{\left\{DS + \frac{N(N-1)}{2}\right\}}{N}$$

In this case, *MaxDS* is the highest possible David's score an individual can have in a group size of  $N$ . The highest-ranking individual of a group can therefore have a David's score of  $N(N-1)/2$ . By dividing the resulting score by  $N$ , the resulting scores have been normalized according to the population under study.

Plotting rank against normalized David's scores in a linear regression will find the best-fitting line for the hierarchy, and the absolute value of the slope,

which ranges from 0-1, can be determined. A perfectly linear hierarchy would yield a slope of -1 (maximum absolute value of 1) (de Vries *et al.*, 2006).

This method is particularly appropriate in that David's score accounts for repeated interactions among group members in the calculation of a hierarchy (Gammel *et al.*, 2003; de Vries *et al.*, 2006). In the case of approach-withdrawal interactions, the proportion of wins and losses is the ratio of approaches that resulted in withdrawal versus those that did not. For the grooming matrix, a loss was counted when a focal animal groomed another, and a win was counted when a focal animal received grooming. de Vries' method corrects for chance between individuals and offers a randomization procedure which compares the results of the group's hierarchy against the steepness based on random chances for all dyads for approaches that result in withdrawals (2006).

Field work has shown that larger females typically obtain an elevated position in their group in mountain gorillas (Harcourt and Stewart, 1987). To see if this was true of western lowland gorillas, I used Spearman's rank correlation to test whether a female's body size, measured by her weight at her last physical (Table 1), was connected to her overall rate of withdrawal from another female as well as to the overall rate at which she was groomed.

### *Stereotypical Behaviors*

Since captivity is known for being conducive to the development of stereotypical or abnormal behaviors, I investigated the occurrence of these in the



group members. In my notes, I recorded each abnormal behavior as a self-directed stereotypical behavior (ST), but made note of the specific action happening. Some of the most common stereotypical behaviors witnessed in captive western lowland gorilla groups are characterized by their unusual and repetitive nature and can include head rolling, regurgitation and reingestion of food (R/R), excessive scratching, and finger sucking, rocking, etc. (Bennett and Fried, 1990; duBois *et al.*, 1991; Lukas, 1999). In addition to keeping track of the frequency and distribution of stereotypical behaviors, I calculated the mean rate of abnormal behaviors per hour per observation block for each focal individual and utilized a Wilcoxon Signed-Rank test to see if those means were different.

## RESULTS

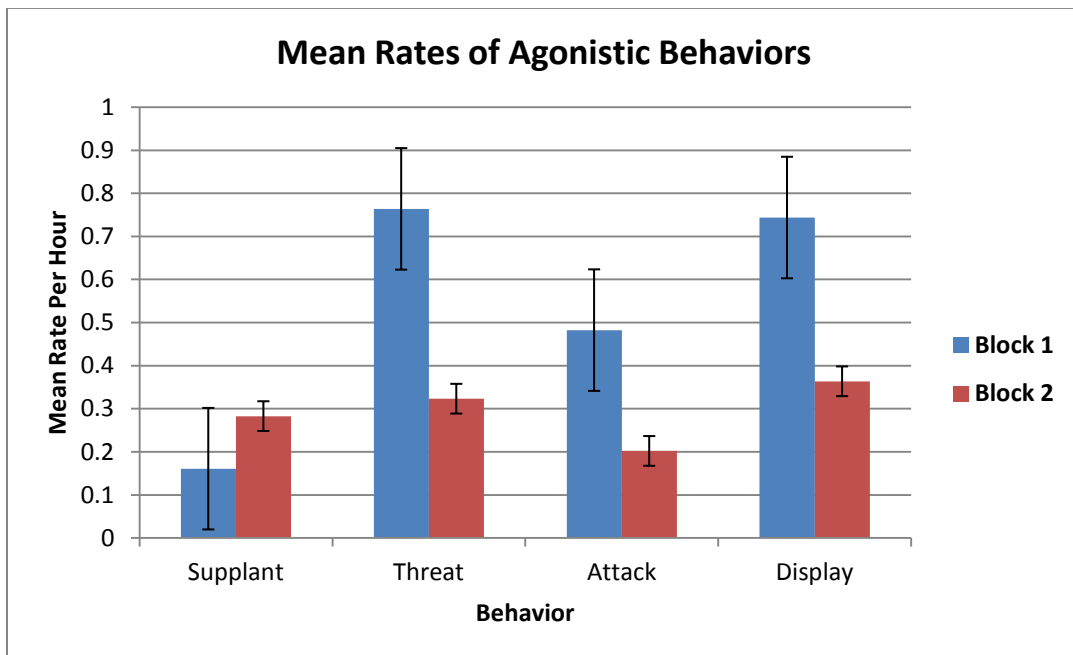
### Rates of Affiliative and Agonistic Behaviors

Mean rates per hour of behaviors were calculated for each of the observed social behaviors on a per block basis. Of the affiliative behaviors, sexual solicitation was the most performed behavior in Block 1 (1.025 instances of solicitation per hour) while sitting in close proximity was seen at the highest rate in Block 2 (2.101 sits per hour). On the other hand, greeting another individual was the least performed behavior in Block 1 (0.020 greetings per hour) and mounting had the lowest rate in Block 2 (0.040 mounts per hour). Mounts were performed exclusively by the adult male, whereas sexual solicitations were performed almost exclusively by females Macy and Kazi.

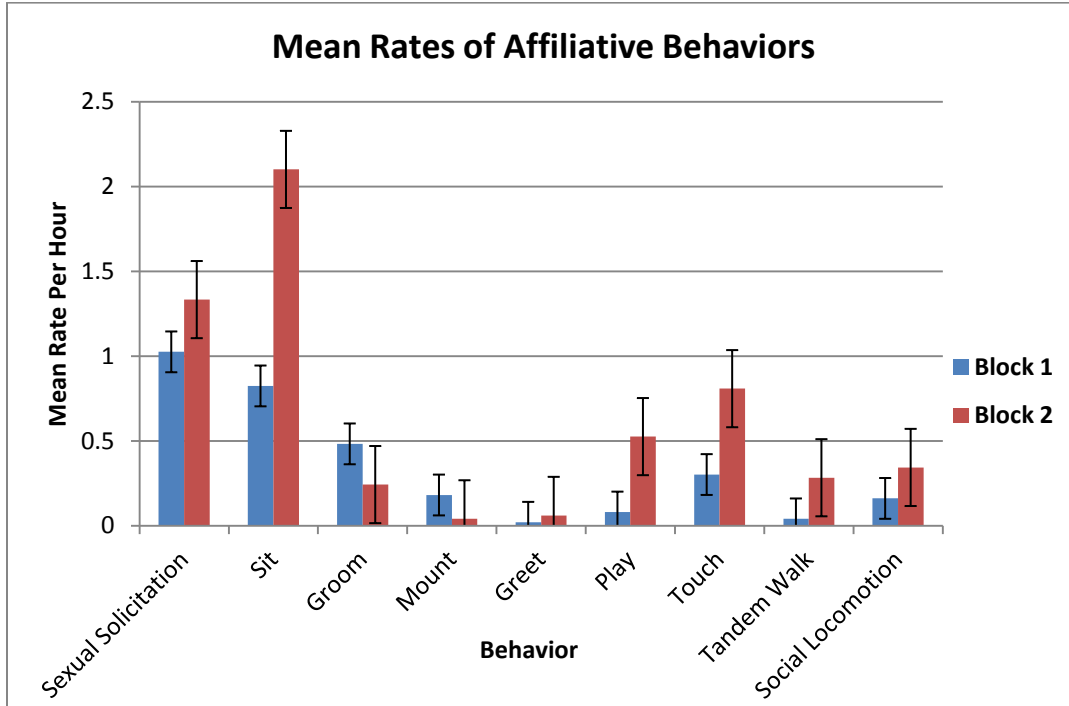
In regard to agonistic behaviors, supplants were the least common agonistic behavior in Block 1 (0.161 supplants per hour) and attacks were lowest in Block 2 (0.202 attacks per hour). Block 1 had the highest rate of threats (0.764 threats per hour) and Block 2 had the highest rate of aggressive displays (0.364 displays per hour) (Figure 4a).

A Mann-Whitney U test compared the distributions of each behavior type across blocks and revealed that there was a significant difference in means in the following behaviors: threat, which was higher in Block 1 ( $U=1894$ ,  $p=0.036$ ), sitting in close proximity ( $U=3046$ ,  $p<0.001$ ), play ( $U=2582$ ,  $p=0.011$ ), tandem walk ( $U=2509$ ,  $p=0.017$ ), and social locomotion ( $U=2558.5$ ,  $p=0.035$ ), all of which were higher in Block 2 (Figures 4a and 4b). Overall, the rate of threats

decreased by more than 50 percent from the first to the second block (Block 1: 0.764 threats per hour; Block 2: 0.323 threats per hour). From the first to the second block, the rate of playing increased approximately 6.5 times between blocks (0.080 plays per hour to 0.525 plays per hour), tandem walking increased approximately seven times (0.040 instances of tandem walking per hour to 0.283 instances of tandem walking per hour), social locomotion increased two times (0.161 instances of social locomotion per hour to 0.343 instances of social locomotion per hour), and sitting in close proximity increased 25 times (0.8241 sits per hour to 2.1010 sits per hour).



**Figure 4a. Mean Rates of Agonistic Behaviors.** Mean rates per hour are presented for each observed agonistic behavior for both observation blocks. Error bars show standard error.



**Figure 4b. Mean Rates of Affiliative Behaviors. Mean rates per hour are presented for each observed affiliative behavior for both observation blocks. Error bars show standard error.**

For the females in Block 1, Macy was most often observed sexually soliciting to Cenzoo (2.113 instances of solicitation per hour). Kazi was seen grooming the most in Block 1 at a rate of 1.633 grooms per hour. Acacia spent most of her time in Block 1 touching other individuals (1.04 touches per hour) (Figure 5a). In the second block, all of the females had the highest rates per hour of sitting in close proximity to another individual (Acacia: 2.640 sits per hour; Macy: 2.776 sits per hour; Kazi: 2.510 sits per hour). (Figure 5b). The adult male was most frequently observed displaying toward the females in both blocks (Block 1: 2.846 displays per hour; Block 2: 1.500 displays per hour).

An Independent Samples Kruskal-Wallis test showed there were differences in means among individuals for virtually every behavior: threat, display, mount, sexual solicitation, sitting in close proximity, play, groom, tandem walk, and touch.

For three of the behaviors, the male drove the differences. The male was responsible for most of the observed threats (35 out of 54 total threats) ( $H=34.807$ ,  $p<0.001$ ). The females' threats were relatively infrequent and evenly distributed across the two observation blocks. Aggressive displays were performed exclusively by the male, which accounts for the significant difference among individuals ( $H=57.214$ ,  $p<0.001$ ). Like the displays, all instances of mounting were performed only by the male ( $H=23.358$ ,  $p<0.001$ ) (Figures 5a, 5b, and 6).

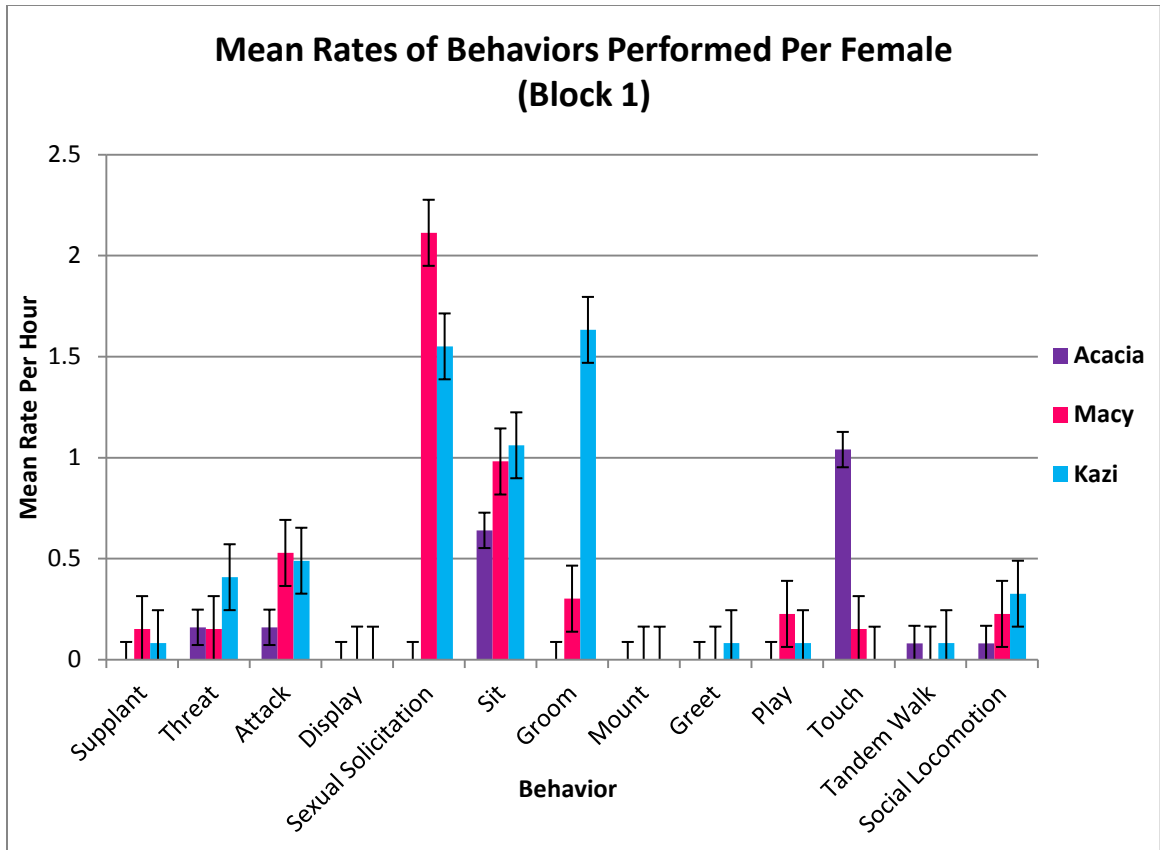
The remaining differences among individuals could be attributed to the females. Macy and Kazi drove the differences seen in sexual solicitation. Kazi was relatively close to Macy's rate of solicitation at 1.551 instances of solicitation per hour. Acacia never solicited and the male solicited at a rate of 0.36 instances of solicitation per hour (9 out of 116 solicitations) ( $H=30.977$   $p<0.001$ ). The means of sitting in close proximity were similar among the females, but the male's rate was much lower ( $H=17.169$ ,  $p<0.001$ ). Similarly, the females played with one another at similar mean rates per hour, but the male was never observed playing ( $H=9.657$ ,  $p=0.022$ ).

Kazi was behind the differences in grooming, her rate being approximately 6 times more per hour than the other females ( $H=32.892$ ,  $p<0.001$ ). The male was never observed grooming. Tandem walking was also only seen in the females. The unrelated female, Acacia, initiated most of this behavior (0.590 instances of tandem walking per hour overall) and her rate was approximately 15 times that of either Macy (0.039 instances of tandem walking per hour overall) or Kazi (0.040 instances of tandem walking per hour overall) ( $H=23.688$ ,  $p<0.001$ ).

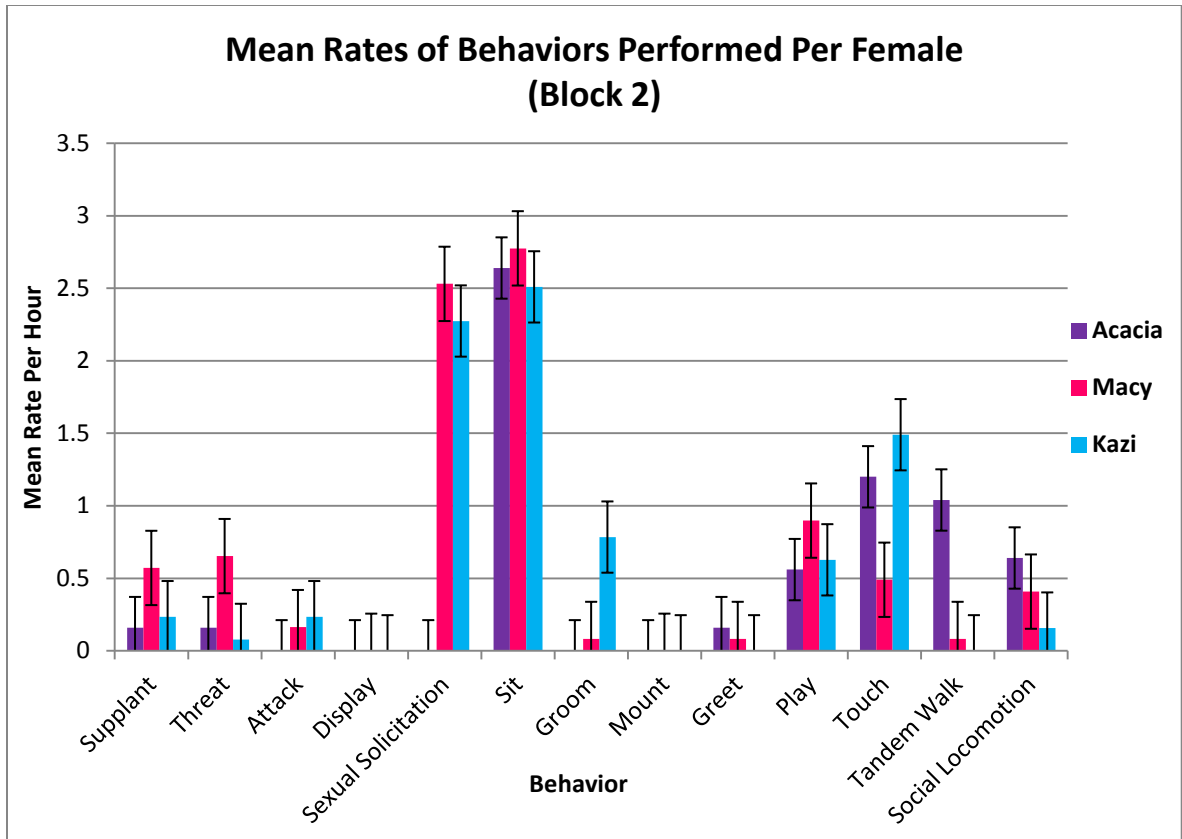
Additionally, Acacia initiated most instances of touching, her rate (1.179 touches per hour overall) being two times as much as Kazi (0.760 touches per hour overall) and four times as much as Macy (0.314 touches per hour overall) ( $H=22.090$ ,  $p<0.001$ ).

From observing females' affiliative interactions, it appeared that there was a connection among sitting in close proximity, tandem walking, touch, and play, as well as between grooming and touch. A Spearman's rank correlation showed that sitting was correlated with touch ( $r_s=0.220$ ,  $p=0.011$ ) and tandem walking ( $r_s=0.223$ ,  $p=0.012$ ). Touch was correlated with play ( $r_s=0.234$ ,  $p=0.006$ ) and tandem walking ( $r_s=0.180$ ,  $p=0.037$ ). Grooming was not significantly correlated with touch ( $r_s=0.076$ ,  $p=0.382$ ).

Additionally, it seemed as though the agonistic behaviors were connected. A Spearman's rank correlation revealed that supplants were correlated with threats ( $r_s=0.209$ ,  $p=0.015$ ), and attack was correlated with threat ( $r_s=0.479$ ,  $p<0.001$ ), as well as with display ( $r_s=0.450$ ,  $p<0.001$ ).

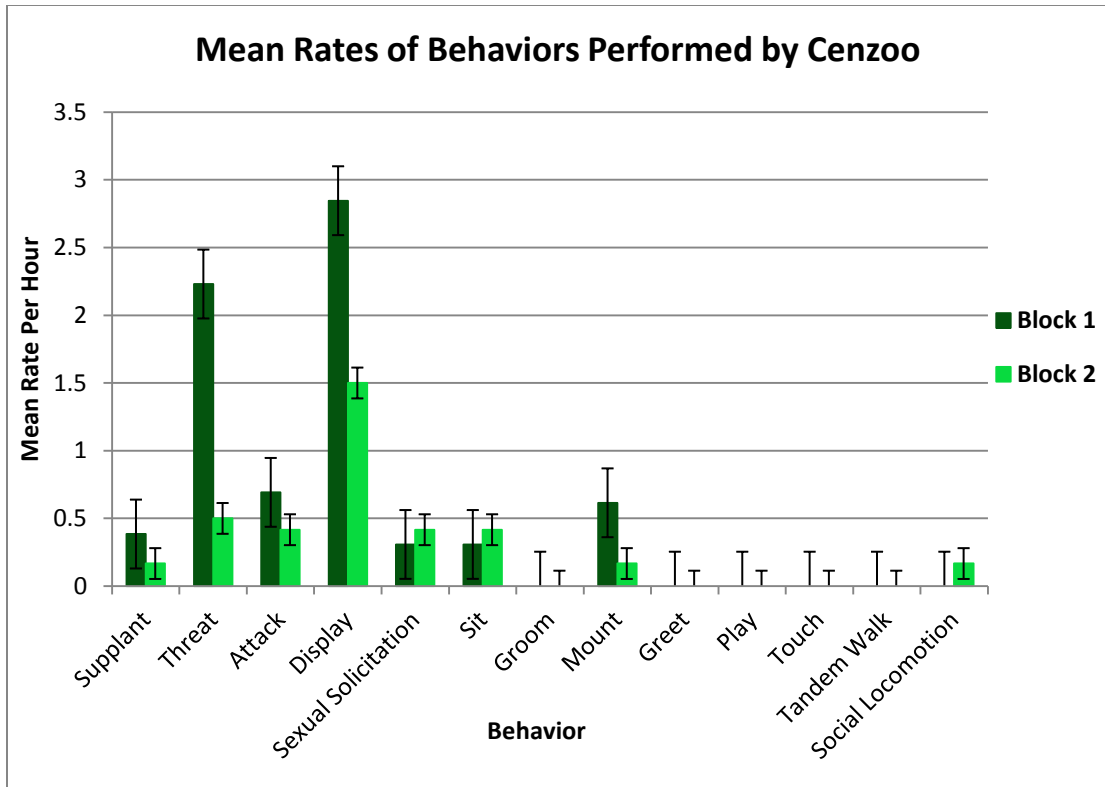


**Figure 5a. Mean Rates of Females' Behaviors in Block 1.** The mean rates per hour of each behavior are shown for each female during the first observation block. Error bars show standard error.



**Figure 5b . Mean Rates of Females' Behaviors in Block 2. The mean rates per hour of each behavior are shown for each female during the second observation block. Error bars show standard error.**





**Figure 6. Mean Rates of Cenzoo's Behaviors. The mean rates per hour of each behavior are shown for the male in both observation blocks. Error bars show standard error.**

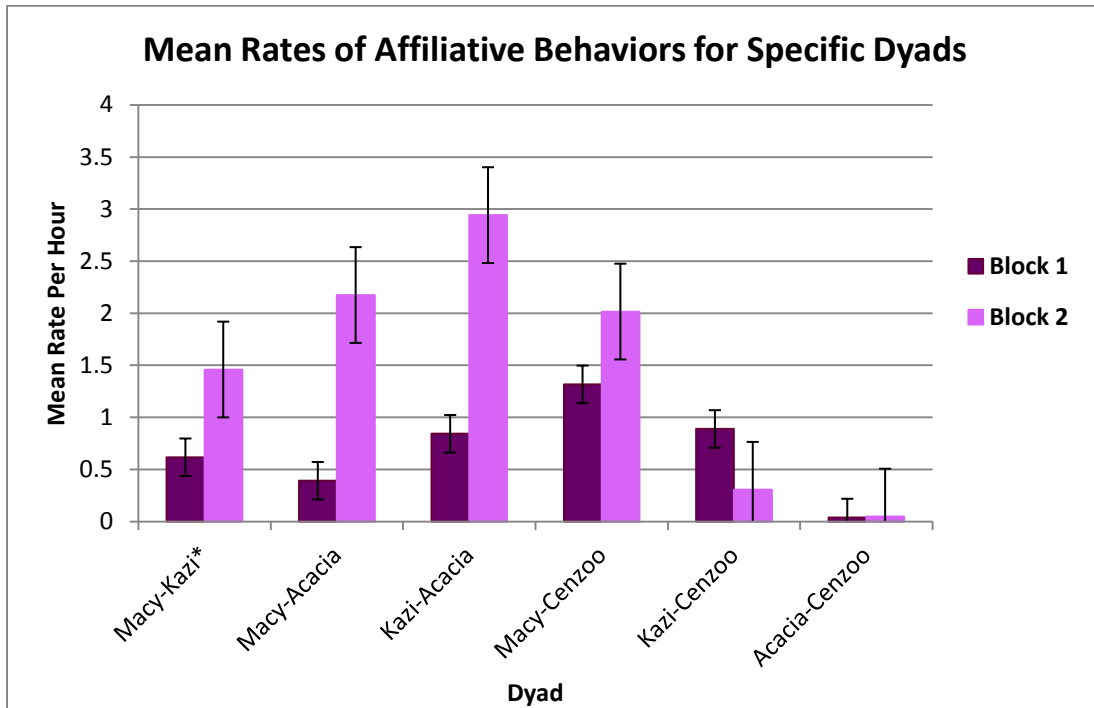
## Dyadic Interactions

A Spearman's rank correlation determined that the rate of affiliative dyadic interactions per hour for all individuals increased with time (in days) over the two observation blocks ( $r_s=0.208$ ,  $p=0.002$ ). Furthermore, the rate of agonistic dyadic interactions decreased with time over the two observation blocks ( $r_s= -0.185$ ,  $p=0.005$ ). These findings were further supported by a Related-Samples Wilcoxon Signed-Rank test, which revealed that there was a difference in affiliative rates ( $Z=1.00$ ,  $p<0.001$ ) and agonistic rates per hour ( $Z=13.00$ ,  $p<0.001$ ) and time.

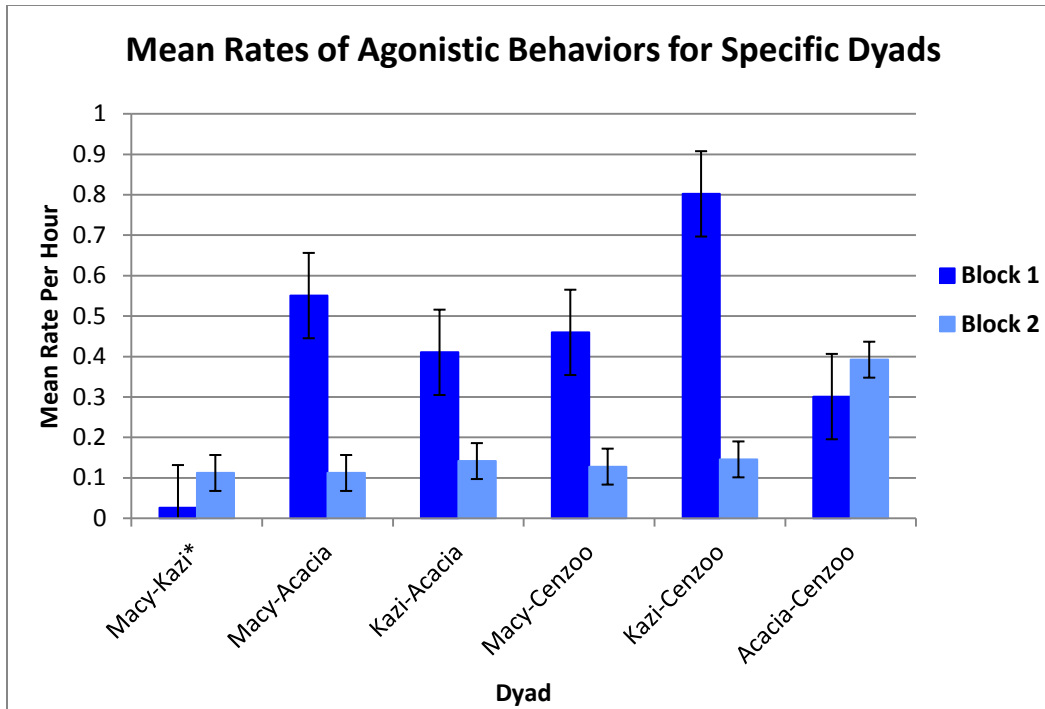
To see if the block had an influence on the correlations seen between time in days and the rates of affiliative and agonistic interactions, I conducted a test for partial correlation in which I controlled for block. Block number did not have any significant effect on either the correlation between affiliative rate and time ( $r_s=0.030$ ,  $p=0.336$ ) or agonistic rate and time ( $r_s= -0.101$ ,  $p=0.079$ ). Since there were correlations between the rates of affiliative and agonistic behaviors and time, I conducted another Spearman's rank correlation to establish whether the patterns of increasing affiliative rates and decreasing agonistic rates were correlated with each other. There was no correlation between these two variables ( $r_s=0.061$ ,  $p=0.195$ ).

Where specific dyads are concerned, Kazi and Acacia had the highest rate of affiliation, while Acacia and Cenzoo had the lowest rate (Figure 7a). The latter

pairing exhibited the highest rate of agonism overall. Macy and Kazi showed the lowest rate of agonism (Figure 7b).



**Figure 7a. Mean Rates of Affiliative Behaviors for Specific Dyads.** The mean rates of affiliative behaviors are shown for the six specific pairs of individuals for both observation blocks. The three female-female dyads are on the left half of the graph and the three male-female dyads are on the right half. Asterisk (\*) denotes half-sister pair. Error bars show standard error.

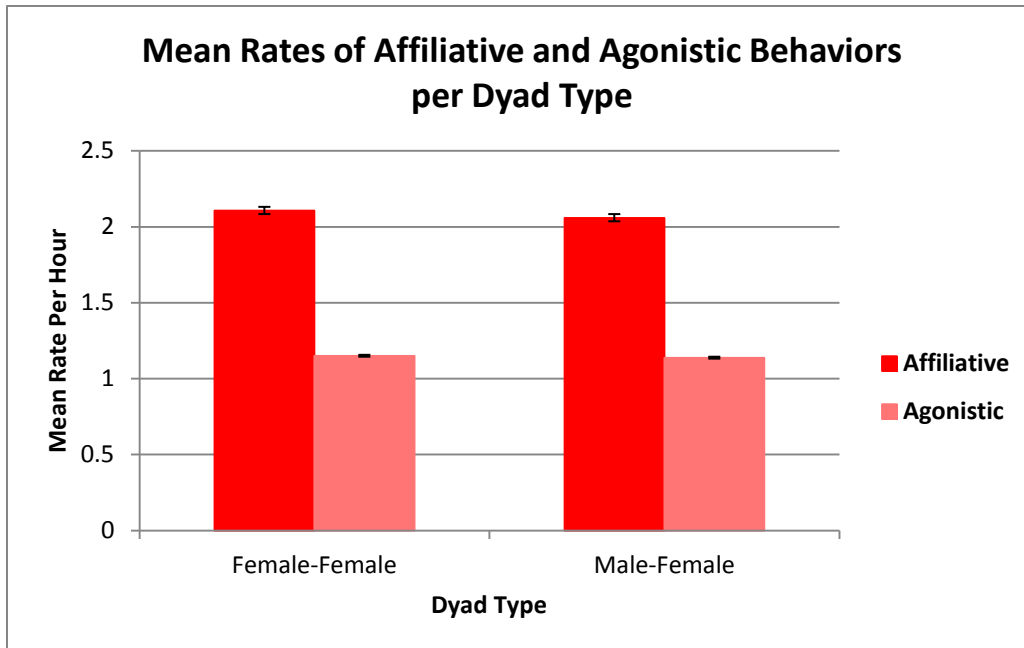


**Figure 7b. Mean Rates of Agonistic Behaviors for Specific Dyads.** The mean rates of agonistic behaviors are shown for the six specific pairs of individuals for both observation blocks. The three female-female dyads are on the left half of the graph and the three male-female dyads are on the right half. Asterisk (\*) denotes half-sister pair. Error bars show standard error.

A Related Samples Friedman Two-Way ANOVA by Ranks determined that there was an overall difference in mean rank (Table 5) of affiliative interactions among all dyads ( $Q=39.401, p<0.001$ ). A Wilcoxon Signed-Rank test showed that among all the dyads, there was no difference in mean ranks between the Kazi-Acacia and Macy-Kazi (half-sisters) dyads ( $Z=-1.925, p=0.054$ ), between the unrelated female dyads Kazi-Acacia and Macy-Acacia ( $Z= -0.837, p=0.403$ ), or between the Kazi-Acacia and Macy-Cenzoo dyads ( $Z= -0.140, p=0.889$ ). However, the Kazi-Cenzoo dyad had a much lower mean rate of affiliation than that of Macy-Kazi ( $Z=-2.200, p=0.028$ ), and was followed by

Acacia-Cenzoo ( $Z=-4.620$ ,  $p<0.001$ ). A Friedman test also showed there was no difference in the mean rank of agonistic behaviors in all the dyads ( $Q=7.144$ ,  $p=0.210$ ).

When specific dyads were grouped into female-female and male-female dyads, the resulting rates of affiliative behaviors and agonistic behaviors across both observation blocks were quite similar. There was a slightly higher rate of affiliation in female-female dyads (1.478 affiliative interactions per hour) compared to male-female interactions (0.858 affiliative interactions per hour). Female-female dyads had a slightly lower rate of agonism (0.140 agonistic interactions per hour) than male-female dyads (0.284 agonistic interactions per hour). Figure 8 shows the means of affiliative and agonistic behaviors by dyad type.



**Figure 8. Mean Rates of Affiliative and Agonistic Behaviors per Dyad Type. The mean rates of affiliative and agonistic behaviors are given for female-female and male-female dyads across both observation blocks. Error bars show standard error.**

I used a Friedman test to determine if there was a difference in the mean rates per hour of affiliative interactions by dyad type (i.e. female-female or male-female). It revealed that among female-female dyads, the mean ranks were the same ( $Q=1.288$ ,  $p=0.525$ ) (Table 5). Conversely, in male-female dyads, mean ranks were different ( $Q= 30.537$ ,  $p<0.001$ ) (Table 5). Each male-female dyad's mean rank value was significantly different from the others (Acacia-Cenzoo/Macy-Cenzoo:  $Z= -4.016$ ,  $p<0.001$ ; Kazi-Cenzoo/Macy-Cenzoo:  $Z= -2.574$ ,  $p=0.010$ ; Kazi-Cenzoo/Acacia-Cenzoo:  $Z=3.634$ ,  $p<0.001$ ). Macy-Cenzoo had the highest rate of affiliation, followed by Kazi-Cenzoo, and Acacia-Cenzoo.

**Table 5. Mean Ranks of Affiliative Behavior For Each Dyad. Mean ranks of affiliative interactions within each dyad are shown in order from largest to smallest, as determined by Related Samples Friedman Two-Way ANOVA by Ranks. Asterisk (\*) indicates female-female dyads.**

<b>Dyad</b>	<b>Mean Rank</b>
Kazi-Acacia*	4.23
Macy-Cenzoo	4.17
Macy-Acacia*	3.77
Macy-Kazi*	3.63
Kazi-Cenzoo	3.25
Acacia-Cenzoo	1.95

### **Female Social Dominance Hierarchy and Steepness of Hierarchy**

#### *Dominance Hierarchy*

The results of the female dominance hierarchy analysis based on approaches and withdrawals in Block 1 determined that Macy was ranked first, Kazi second, and Acacia third. The matrix showed that Acacia withdrew the most from the approaches of Kazi; Macy never approached Acacia except to sit in close proximity, from which Acacia did not withdraw. These interactions with Macy were not considered as dominance and were instead counted as affiliative behaviors. Kazi withdrew only from Macy. Macy did not withdraw from either female; each approach by another female was to sit in close proximity to her (Table 6a).

**Table 6a. Female Dominance Matrix for Block 1.** The dominance matrix shows the mean rates per hours of approach and withdrawal. Approaching individuals are listed in columns and withdrawing individuals are listed in rows.

		Rates focal animal approached an individual		
		Macy	Kazi	Acacia
Rates focal animal withdrew from approaching individual	Macy		0	0
	Kazi	0.0654		0
	Acacia	0.0392	0.0728	

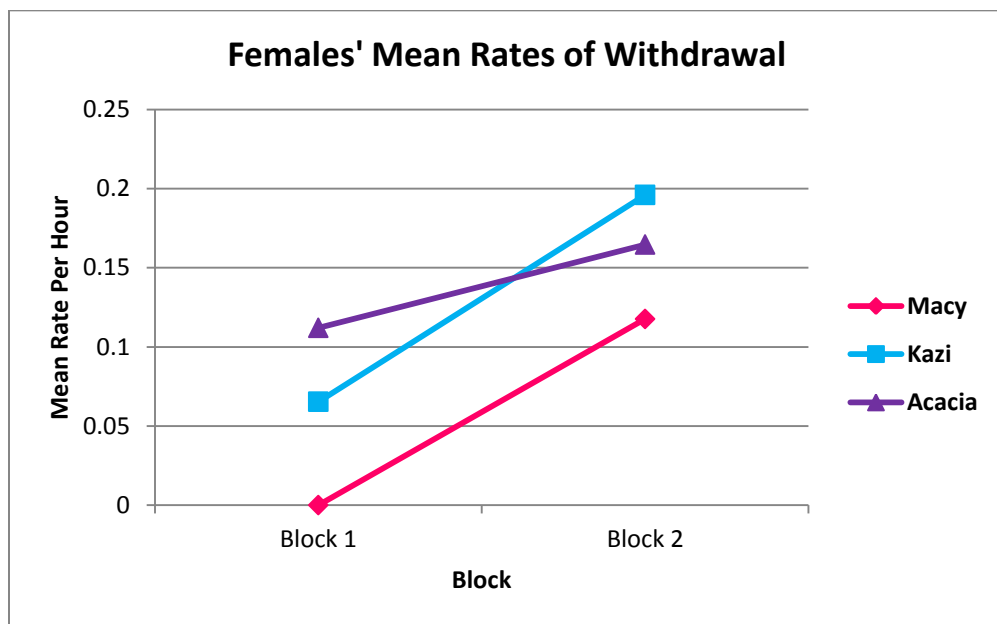
Block 2 rates ranked Macy first once again, although her rate of withdrawal was noticeably more than that of Block 1. Acacia was second-highest, and Kazi obtained the lowest overall status (Table 6b).

**Table 6b. Female Dominance Matrix for Block 2.** The dominance matrix shows the mean rates per hours of approach and withdrawal. Approaching individuals are listed in columns and withdrawing individuals are listed in rows.

		Rates focal animal approached an individual		
		Macy	Acacia	Kazi
Rates focal animal withdrew from approaching individual	Macy		0	0.1177
	Acacia	0.1177		0.0471
	Kazi	0.1177	0.0784	



Each female's mean rate of withdrawal for both observation blocks, (shown in Tables 6a and 6b), are plotted in Figure 9 for comparison. Despite the apparent changes in rank, the mean rates of withdrawal for each of the females were not different, as determined by a Wilcoxon Signed-Rank test ( $Z = -1.342$ ,  $p = 0.180$ ). Landau's index of linearity,  $h = 1$ , indicated a linear relationship in the first and second blocks.



**Figure 9. Females' Mean Rates of Withdrawal.** The line graph compares each female's rate of withdrawal when approached over the two observation blocks.

Many of the observed approaches and withdrawals were in response to the male's presence ( $n = 27$ ). Many of the females approached in order to solicit, and then withdrew when he displayed, mounted them, or showed aggression. These were not factored into the female dominance matrix, as they did not provide any

information about the females' social status. Instead, they were included in the counts of affiliative behaviors as sexual solicitations.

For two of the females, the presence of the male resulted in approximately twice the rate of withdrawal upon his approach for two than was seen in any female-female approach-withdrawal interactions (Acacia: With Male= 0.2403 withdrawals per hour, Without Male=0.1383 withdrawals per hour; Macy: With Male=0.1345 withdrawals per hour, Without Male=0.0588 withdrawals per hour). Kazi's rates of withdrawal were very close in mean, regardless of the male's presence (With Male= 0.0992 withdrawals per hour, Without Male=0.1307 withdrawals per hour). The results of the Wilcoxon Signed-Rank test indicated that the differences in mean rates of withdrawal were not significant ( $Z = -1.064$ ,  $p = 0.109$ ).

Each female's rates of being groomed are detailed in Tables 7a and 7b. In Block 1, Acacia was the most-groomed individual (3.500 grooming attempts received per hour), followed by Kazi (1.667 grooming attempts received per hour), and Macy was last (0 grooming attempts received per hour). In Block 2, Acacia was still the most-groomed individual, and her mean rate of being groomed more than doubled (7.556 grooming attempts received per hour). Macy was the second-most groomed individual, jumping from not being groomed at all in Block 1 to averaging 3.167 grooming attempts received per hour. Kazi's rate of being groomed changed only slightly (1.333 grooming attempts received per hour), but she was ranked last (Figure 10).

**Table 7a. Female Grooming Matrix for Block 1. Mean rates per hour of grooming among females in Block 1. Grooming individuals are listed in columns and individuals being groomed are listed in rows.**

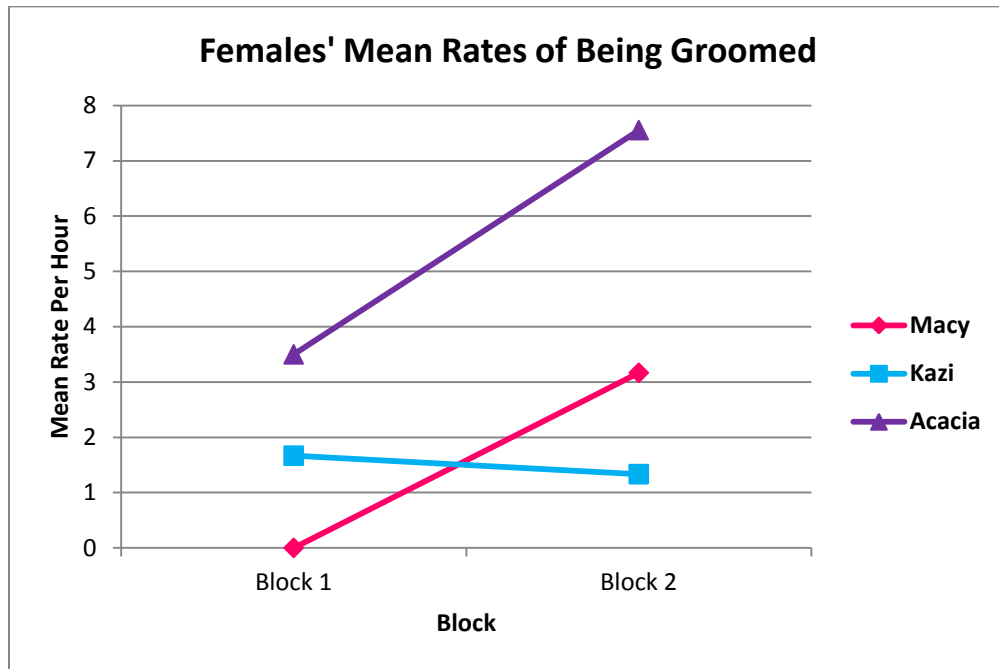
		Rates focal animal groomed another		
		Acacia	Kazi	Macy
Rates focal animal was groomed by another individual	Acacia		3.500	0
	Kazi	0		1.667
	Macy	0	0	

**Table 7b. Female Grooming Matrix for Block 2. Mean rates per hour of grooming among females in Block 2. Grooming individuals are listed in columns and individuals being groomed are listed in rows.**

		Rates focal animal groomed another		
		Acacia	Macy	Kazi
Rates focal animal was groomed by another individual	Acacia		2.889	4.667
	Macy	0		3.167
	Kazi	1.333	0	

Figure 10 depicts changes in each female's mean rate of grooming for both blocks. A Wilcoxon Signed-Rank test determined that the means for each female

between the two blocks were not significantly different ( $Z= 3.00$ ,  $p=1.00$ ). In both blocks, Landau's index was  $h=1$ , indicating a linear dominance relationship defined by bouts of grooming.

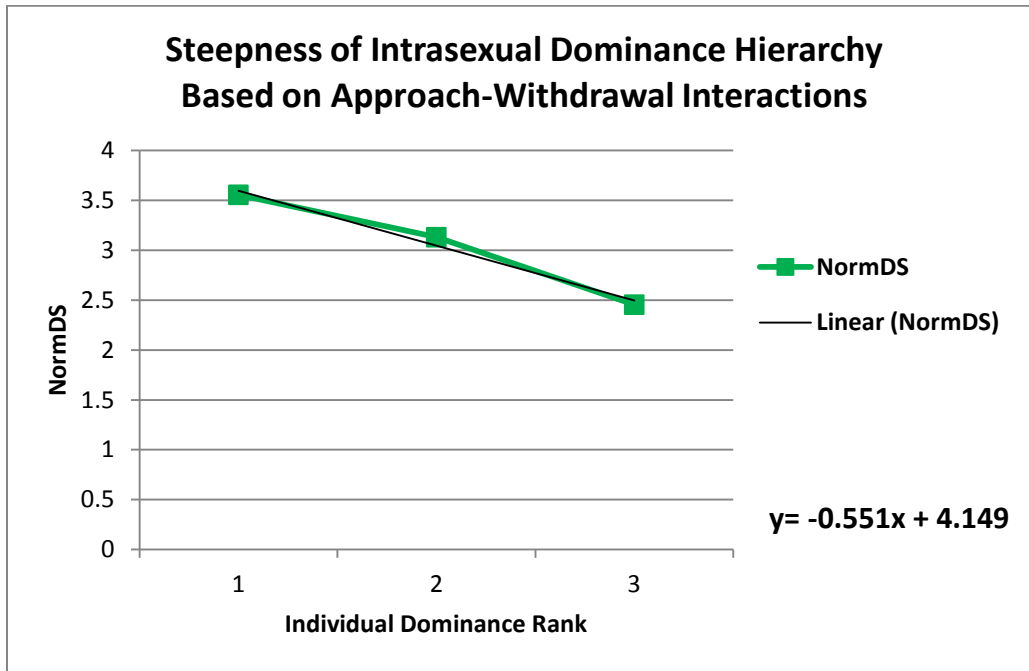


**Figure 10. Females' Mean Rates of Being Groomed.** Mean rates of being groomed per hour are shown for each female for both observation blocks.

### *Hierarchy Steepness*

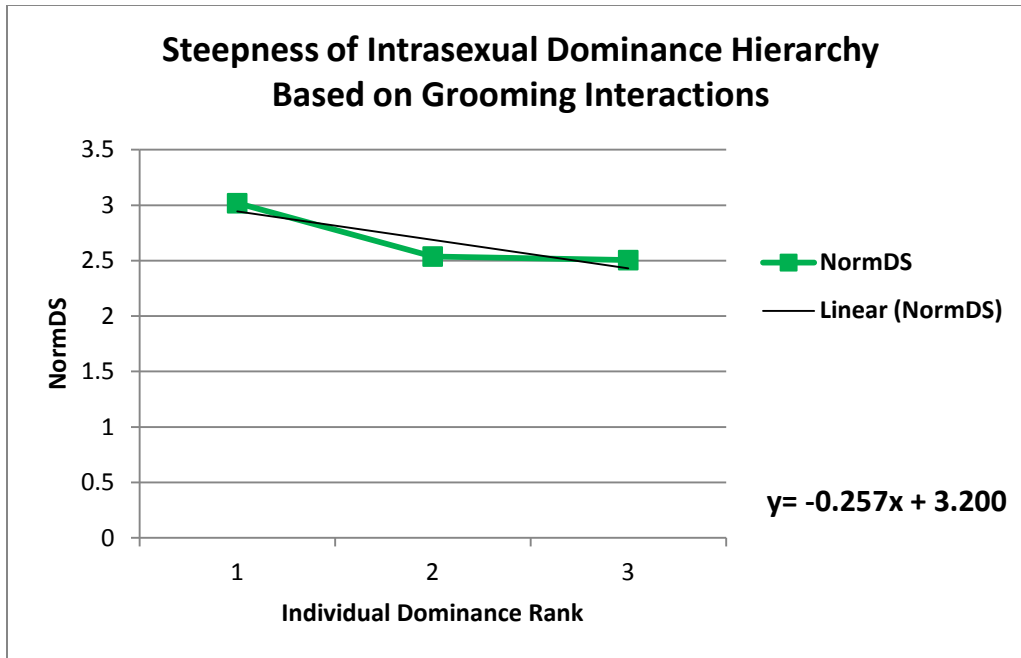
In approach-withdrawal interactions, normalized David's scores ranked Macy first, Kazi second, and Acacia third. A linear regression showed that the resulting hierarchy was not steep with an absolute slope of 0.551. Also, there was no significant relationship between a given female and her rank ( $r=0.991$ ,  $p=0.083$ ) (Figure 11). The possible relationship between body size and status was tested and there was no apparent correlation between a female's body size and her

rank in either of the observation blocks (Block 1:  $r_s=0.400$ ,  $p=0.300$ ; Block 2:  $r_s=0.211$ ,  $p=0.395$ ).



**Figure 11. Steepness of Intrasexual Dominance Hierarchy Based on Approach-Withdrawal Interactions. Steepness of hierarchy was evaluated by plotting normalized David's scores (NormDS) against females' ranks ( $p=0.083$ ).**

Based on grooming interactions, Acacia was ranked first as the most groomed individual, Kazi second, and Macy third in accordance with their calculated normalized David's scores. The linear regression produced a shallow hierarchy and an absolute slope of 0.257. It was determined that there was no significant relationship between a female and her given rank ( $r=0.893$ ,  $p=0.297$ ) (Figure 12). Also, rank according to grooming interactions was not correlated with body size in either observation block (Both blocks:  $r_s=0.500$ ,  $p=0.667$ ).



**Figure 12. Intrasexual Dominance Hierarchy Based on Grooming Interactions. Steepness of hierarchy was evaluated by plotting normalized David's scores (NormDS) against females' ranks (p=0.297).**

### Stereotypical Behaviors

Abnormal behaviors occurred infrequently over the course of the study and were all performed by the females. Acacia and Kazi had the same frequency of abnormal behaviors, 14, over the two blocks, whereas Macy only engaged in an abnormal behavior once. The adult male, Cenzoo, did not exhibit any abnormal behaviors. Interestingly, Acacia exclusively performed the stereotypical head roll and Kazi was only observed regurgitating and reingesting her food (R/R). Macy behaved abnormally only once, where she regurgitated and reingested food. Analysis of the rate of abnormal behaviors revealed no difference between the two observation blocks ( $Z = -0.447, p = 0.655$ ).

# DISCUSSION

## Factors Influencing Social Organization

By undertaking this study, I sought to shed light on the nature of the development of social behaviors in newly-formed gorilla groups. By studying the individual females and the group as a whole, I gained further insight into the quality of the group's interactions as well as how individuals can maximize their wellbeing as part of a group. Specifically, I wanted to see how the group's rates of affiliative and agonistic behaviors changed over time, whether a female dominance hierarchy resulted, and whether the rates of stereotypical behaviors decreased with time.

Dyadic interactions vary a great deal depending on the individuals involved. Interactions within a dyad are at the heart of social organization, as they form the patterns behind long-term relationships (Hinde, 1976). Social behaviors contribute to an organism's resource acquisition which can include anything from food to mates, as well as survival through predator avoidance and care of offspring (Harcourt and Stewart, 1987; Harcourt and Stewart, 2007). Typical behavioral patterns, along with group composition, help individuals maximize reproduction and adapt to cope with selective pressures, either from the environment or other animals. It is important to note that all social animals exhibit some degree of behavioral plasticity, which allows them to modify their behaviors in the event that conditions require such flexibility (Hinde, 1976).

Primates exhibit some of the most complex social groups among mammals. In some species of monkeys, dominance rank is central to group organization, whereas in the great apes, rank plays a diminished role (Cheney, 1992; Harcourt and Stewart, 2007; Scott and Lockard, 1999).

Western lowland gorillas spend virtually all of their time in groups. Females rarely leave them except to join another, and thus form close bonds with group mates. Males without a group of females usually will reside with other males. Group life is central to this subspecies, and the slight behavioral variations found among individuals are paramount in understanding what makes a group successful both socially and reproductively. Examination of my particular study group revealed social patterns characteristic of what has been observed in the wild and in populations of captive western lowland gorillas (Harcourt and Stewart, 1897, 2007; Parnell, 2002; Robbins, 2004; Scott and Lockard, 1999; Watts, 1994).

### **Rates of Affiliative and Agonistic Behaviors**

My hypotheses that each individual's rates of affiliation would increase and rates of agonism would decrease with time were supported. However, there was no correlation between the rates of affiliative and agonistic behaviors because these behaviors did not change at the same rate. These results indicate that in this group of gorillas, the performance of affiliative and agonistic behaviors are independent of one another.



### *Affiliative Behavior Among Females*

Many of the affiliative social behaviors occurred much more frequently in the second observation block probably as a result of reduced group tension and increased familiarity. Tandem walking was one such behavior that mostly occurred in Block 2 and was only seen among the females. The behavior mostly occurred when Cenzoo entered Acacia's line of vision. She would put her arms around another female's waist and proceed to move away from Cenzoo, even if he was not directly approaching her. It is interesting that Acacia incorporated an affiliative interaction with another female into what was essentially a withdrawal from the adult male. Perhaps this was because Acacia may have been looking for support in her avoidance of Cenzoo. It is not surprising that Acacia sought to avoid Cenzoo in so many cases, given the lack of affiliative interactions between the two. In Block 1, Acacia received many threats and attacks from the male.

Tandem walking was positively correlated with other affiliative behaviors, including touching and sitting in close proximity. The rates of sitting in close proximity almost doubled for each of the females from the first observation block to the second, but the differences were not significant. However, the fact that there was such an increase indicates the females' increasing comfort with one another as members of the same group. The correlation between tandem walking and sitting could be due to the fact that Acacia would often terminate sitting with the other females at the site of Cenzoo and would then proceed to tandem walk away.

Strengthened bonds are likely also behind the differences in touching. The frequency of touches increased in the second block. Acacia had the highest rate of touching among all the females, and this behavior was often seen before she initiated a bout of tandem walking. It appears as though Acacia used touching predominantly as a signal to the other females to join her as she attempted to avoid the male.

The connection between tandem walking, touching, and sitting in close proximity can likely be attributed to Acacia's search for support in avoiding the male. Touching and sitting with the other females more frequently could have helped Acacia strengthen social ties with the females so they would more readily spend time with her. Given Acacia and Cenzoo's aggressive relationship in the first block, Acacia may have looked to the other females for protection. In agonistic situations, it is possible that interaction with other individuals could redirect or reduce aggression. Interacting with the supposed intent of lessening aggression has been witnessed in mountain gorillas and chimpanzees (de Waal and van Roosmalen, 1979; Harcourt and Stewart, 1987; Harcourt and Stewart 2007; Watts, 1995).

Touching was also correlated with play behavior among the females. Touches between Macy and Kazi often led to a bout of play. In the first block, only Macy and Kazi played with each other, which is likely due to their familiarity with each other from being raised in the same family group since

infancy. In Block 2, Acacia joined the half-sisters in bouts of play, likely due to the social bonds that had resulted from just a few months of living as a group.

### *Sexual Behavior*

There was noteworthy asymmetry among sexual behaviors within the group. Sexual solicitation rates differed among individuals but remained fairly constant over the two blocks. Among females, Macy solicited at the highest rate, followed by Kazi. Acacia was never observed to solicit. Cenzoo reciprocated occasionally and would solicit the females, but his overall rate was five to six times less than that of either Macy or Kazi. Cenzoo's preferences of females increased with increased rates of solicitation. Macy exhibited the highest rate of solicitation and she was most preferred by Cenzoo, as shown through his increased frequency of mounting attempts and reciprocated solicitations. Mounting was exclusively initiated by Cenzoo. These displays often followed a solicitation by one of the females, although Cenzoo sometimes ignored such advances, especially coming from Kazi.

### *Male Agonistic Behaviors*

Aggressive displays are specific to males, and Cenzoo frequently used these to assert his dominance over the females, presumably to impress his mates. Similarly, Cenzoo was responsible for the majority of threats, which usually occurred after displaying to a female. Interestingly, displays and threats were not

correlated with each other, but they were both positively correlated with attack. In several cases, Cenzoo would either threaten or display to a female (or to all three of them) and would proceed to slap, kick, or bite them if they did not respond. The noticeable decrease in threats from the male between blocks can be explained by increased familiarity. Cenzoo arrived at Riverbanks unacquainted with the three females. Moreover, Cenzoo previously lived in groups with other males and also spent time living as a bachelor male (Brian Goleman, Keeper of Gorillas/Small Mammals, and Emily Lopez Guertin, Senior Keeper of Gorillas/Small Mammals, personal communication). The novelty of the living situation at Riverbanks could have instigated Cenzoo's need to exhibit dominance in all its forms. In the first few weeks following introduction, Cenzoo frequently acted agonistically, apparently to remind the females of his status as the dominant silverback. With time, this was not as necessary because of his increased association with the females.

In addition, Riverbanks houses a lone male, Patrick, in the same indoor enclosure. It is possible Cenzoo felt threatened by the presence of the male and therefore displayed his dominance in order to win over the females. After a while, Cenzoo probably learned that he had exclusive access to the females and did not need to assert his dominance as much.

### *Female-Female Agonism*

There were also several instances of female-female threatening, although much less frequent than threats from the male. Possible explanations for the infrequency of threats include prior acquaintance and the need to maintain close ties. Since the half-sisters were raised together, they were used to interacting with each other. Threats were most often seen in interactions with the unrelated female, most likely due to the lack of prior contact. In wild gorilla groups, females spend a great deal of time together and frequent aggression can damage the bonds between individuals (Harcourt and Stewart, 1987; 2007).

### *Supplants*

One behavior that plays a central role in gorilla society is supplanting another individual. Especially in females, supplanting is used to advertise one's elevated status and either culminates in the lower-ranking female's loss of her spot or food resources. In contests of dominance, related females can form kin-based alliances to be more successful in these situations, provided they have another related female in the group (Harcourt and Stewart, 1987; Scott and Lockard, 2007). The majority of information gathered on the importance of supplanting comes from mountain gorilla populations, but existing work has verified the significance of this behavior in populations of captive western lowland gorillas as well (Harcourt and Stewart, 2007; Scott and Lockard, 1999; Scott and Lockard, 2007).

In the group at Riverbanks, instances of supplants involved an approaching individual taking another's nesting material or Cenzoo taking the sitting place of a female. In very rare events, a female would push another female out of her place. Observations of wild western lowland gorillas have also shown that instances of supplants in female-female interactions to be low (Stokes, 2004). Taking another's nesting material was the most common cause of supplants, and this is likely due to its short supply in the outdoor enclosure. In all the observed cases of supplants, further aggression was not seen. However, supplants were often preceded by threats, which can account for the correlation between the two behaviors. Supplanting females from their sitting place was one way Cenzoo asserted his role as dominant silverback in the group and this is typical of male behavior within wild single-male gorilla groups (Harcourt and Stewart, 2007; Stokes, 2004).

### **Dyadic Interactions**

The lack of a difference among mean rates of agonistic interactions among dyads can be attributed to two factors. First, there was little agonism overall in female-female dyads. Second, the means of Cenzoo's agonistic interactions with each of the females were fairly close. Much of this agonism occurred in Block 1, where Cenzoo frequently displayed, threatened, and attacked the females. In agreement with my results, the work of Stokes (2004) showed that male-female relationships exhibit a much higher rate of agonism as opposed to female-female

interactions, and the levels of agonistic interactions are fairly consistent among dyads.

In contrast, the rates of affiliation differed among dyads, particularly in male-female dyads. The dyad mainly responsible for this difference was that of Macy and Cenzoo, which had the highest rates of affiliation among the male-female dyads. It is possible that Macy's solicitations are at least partly responsible for this. As stated before, Macy's rate of sexual solicitation was the highest among the females and constituted more than half of the total solicitations observed (59 out of 116 total solicitations). The male's responses in terms of reciprocated solicitations and mounting were not as frequent as Macy's solicitations, but they were much more numerous than his affiliative responses to the other two females (6 out of 10 mounts of Macy and 5 out of 9 solicitations to Macy). This is reflected in his rates of affiliation with the other two females, which are the two lowest among all six possible dyads. Evidently, bonds between females and the group's male were not as strong as those in female-female dyads, and this is typical of wild gorillas (Harcourt and Stewart, 1987; Harcourt and Stewart, 2007; Parnell, 2002).

Overall, rates of affiliation were similar within the three female-only dyads, but the highest rate was observed between Kazi and Acacia. These two females were frequently together during the latter half of the study, when Macy was shifting her focus to Cenzoo. The fact that the Kazi-Acacia and Macy-

Cenzoo dyads statistically had the highest rates of affiliation with one another corresponds with the developing patterns of relationships in the group over time.

In female transfer societies, it has been suggested that kin selection is diminished since females do not stay with their relatives in their natal groups. In gorilla groups, females are usually much more tolerant of kin than non-kin (Harcourt and Stewart 1987; 2007), but most interaction with kin occurs in the natal group. In my study group, increased affiliation with the unrelated female, especially in Block 2, is representative of the interactions that might be seen in other female transfer species. Glander (1980) suggested that nepotistic relationships do not play much of a role in societies where one or both sexes routinely transfer, as is the case with mantled howler monkeys (*Alouatta palliata*).

### **Dominance Hierarchies**

Dominance hierarchies are a part of group life in many socially complex species and these result from disparities in such qualities as size, age, physical strength, and personality. These disparities lie at the root of intra-group competition. Within a social group, the individuals whose behavior is not governed or limited by others are dominant. When it is determined that individual A is dominant over B, the observed relationship often sets the stage for future interactions between individuals and gives strong predictive value to the outcome of competitive events (Leonard, 1979).



Western lowland gorilla society is not as rigidly structured as some other primates species, but there has been some evidence of female dominance hierarchies from field studies (Harcourt and Stewart, 1987; 2007). Despite this, there have not been enough long-term field or captive studies to truly validate the significance of the role rank plays in gorilla society (Robbins *et al.*, 2005). A key question I wanted to address was whether a female dominance hierarchy would develop in the newly-forming group at Riverbanks. Incorporating methods from field and captive studies, I evaluated female rank in terms of approach-withdrawal interactions and grooming.

While approach-withdrawal interactions did produce a hierarchy with Macy as the alpha female, Acacia and Kazi switched rank between blocks. This inconsistency can be attributed to the nature and number of the approaches as well as personality differences. Withdrawals by females were rare, occurring just four times. The unrelated female, Acacia, was responsible for three of these, two in the first block, and one in the second. Kazi withdrew from Macy once in the first block. For this group to exhibit a truly stratified social structure based on submission of other individuals in the group, there should have been a much greater number of approaches that resulted in withdrawals. The infrequency of these interactions in my study subjects make approach-withdrawals alone an essentially ineffective way to analyze female social stratification.

Most approaches resulted in affiliation rather than withdrawal and frequently resulted in two females sitting within one meter of each other for a

prolonged period. Withdrawal in female-female interactions were rarely accompanied by submissive behaviors (crouching away from an individual, tucking in one's limbs, not meeting another's gaze) (Harcourt and Stewart, 2007; Watts, 1994). In cases where Acacia was approached by another female, her withdrawal appeared to be the result of disinterest in the approaching individual. No aggressive interactions took place immediately before the older, unrelated female's withdrawals.

Contrary to female-female approach-withdrawal interactions, when a female withdrew from the silverback it seemed to be in an attempt to avoid further aggression. Typically, females submit to a male after a dominance display or an agonistic encounter, and this was often the case in the Riverbanks group. Sometimes, the male would display or threaten after he was solicited to by a female. Over time, the instances of male-female agonism decreased, but the females' responses to the male did not. When either Macy or Kazi were threatened, both females would usually would back off, but sometimes remain within 5 meters. They would often resume soliciting the male after a minute or so or stare intently at him with their arms crossed. From the first to the second blocks, Macy and Kazi's approach-withdrawal interactions did not change much.

On the other hand, Acacia's withdrawals from Cenzoo increased in frequency in the second observation block. At the beginning of the study, Acacia kept her distance from Cenzoo, probably due partly to the high rate of agonistic interactions relative to affiliative interactions. In the second block, Acacia spent

more time in much closer proximity to Cenzoo, allowing them more direct interaction. Furthermore, Cenzoo attempted to peacefully interact with the females much more in the second block. Overall, he reduced his of agonistic behaviors and on several occasions tried to affiliate with the females by sitting in close proximity to them, in which case Acacia would tandem-walk away with another female. Despite this, the females' rates of withdrawal in the presence of the male were not statistically different than those of female-female interactions. The low rates of withdrawal in male-female interactions show how little the male interacted with the females, outside of mating or showing aggression, the latter of which was a presumed illustration of dominance. This pattern of male-female interaction is in accordance with the descriptions of wild populations (Harcourt and Stewart, 2007; Parnell, 2002; Stokes *et al.*, 2003).

Grooming has been suggested as a way to enhance group cohesion and reinforce social roles in groups (Cheney, 1992). While gorilla group members do not groom one another as regularly or as intensely as some other primate societies, grooming still serves the same purpose (Harcourt and Stewart, 2007). In the wild, it is common for the older females to be more often groomed by younger, lower-status females (Harcourt and Stewart, 2007; Parnell, 2002; Stokes, 2004).

When grooming was taken into account in my study group, the normalized ranks awarded to each female were markedly different from those produced in the analysis of approach-withdrawal interactions (Approach-withdrawal: Macy (1),

Kazi (2), Acacia (3); Grooming: Acacia (1), Kazi (2), Macy (3)). As with observations from field studies, the older female in the Riverbanks group, Acacia, was groomed most often. Interestingly, the half-sisters experienced a reversal of rank between the two blocks due to Macy's increased grooming of Acacia in the second block.

Since Macy and Kazi were already acquainted prior to group formation, it was unlikely grooming was needed to establish or strengthen their relationship. Since Acacia was unrelated and physically larger, it could be that Macy and Kazi sought to establish a relationship with her in this way. This was particularly important for Kazi, as Macy shifted her focus to Cenzoo in the months following group formation.

An important point is that grooming was not correlated with any other affiliative behavior. This could be the case because grooming was not normally a behavior that preceded or followed another affiliative behavior. For example, grooming did not normally take place after an individual touched another. Nonetheless, there was still one specific instance of grooming immediately following a certain sequence of behaviors. On the last day of Block 1, Kazi solicited Cenzoo and he responded by mounting. At one point Kazi moved slightly and Cenzoo attacked her by dragging her across the outdoor enclosure and biting her foot. Kazi immediately ran to her half-sister, who began grooming her in an apparent attempt to comfort her. This particular event shows that grooming is a way to fortify connections between group members and calm those

in distress. Grooming serves this same function in several species of monkeys, including baboons and macaques, as well as in other apes like chimpanzees (de Waal, 1989; Henzi and Barrett, 1999; Lehmann *et al.*, 2007; Terry, 1970). In fact, grooming has been shown to reduce tension and heart rate in primates and other mammals like cattle and horses (Dunbar, 1991; Feh and de Mazières, 1993; Sato and Taramizu, 1993).

It has been established that increased body size in female gorillas is related to social status (Harcourt and Stewart, 1987). Despite this connection, other work has suggested that younger females, which are generally smaller and more agile, can gain a competitive advantage in certain situations (e.g. food acquisition) (Scott and Lockard, 1999). In the Riverbanks females, body size was not correlated with rank according to rates of withdrawal. Resource competition was not a major factor in my study due to dispersed distribution of nutritional resources, which likely explains the lack of a correlation between rank and body size.

Since body size is an indicator of age and possibly experience, it is surprising that the rate of being groomed was not significantly correlated with a female's weight in my study. Nevertheless, Acacia, the oldest female, had the highest mass (78 kg) of the females, and based on the fact that she was groomed frequently by the younger two females, which agrees with the observations of previous studies of gorillas (Fischer and Nadler, 1977; Harcourt and Stewart, 1987; Harcourt and Stewart, 2007).

Acacia was most frequently groomed by Kazi. The fact that Macy and Cenzoo spent most of their time engaging in sexual behaviors with one another was likely a significant adjustment for Kazi, who has spent time with Macy since birth. Kazi, in grooming Acacia, may have been trying to form a close bond with the only other individual in the group who was available. Consequently, Kazi and Acacia were almost always in each other's company during the entirety of the second block.

### **Strength of Female Dominance Relationships**

Landau's index of linearity, used to assess the strength of dominance relationships, indicated a linear dominance relationship among the females, but the rankings based on comparing grooming and approaches and withdrawals did not match. In the cases of grooming and approach-withdrawal in both blocks, it is likely that the Landau's index values resulted in a perfectly linear relationship due to the fact that there were so few individuals included. The lack of steepness observed in both hierarchies indicated that no strong, stratified relationship had yet formed among the females in the study group. The outcomes of certain dyadic interactions may point to a "winner," but these outcomes are not numerous enough to give any female a definitive ranking. These findings agree with what has been found in captive and wild groups (Robbins *et al.*, 2005; Scott and Lockard, 1999; Watts, 1994).

It was hypothesized that the related females in the group would rank higher than the unrelated female due to the formation of a kin-based alliance as well as to clumped and defensible resource distribution in the outdoor enclosure. Due to the contradictory information returned from the two matrices and their lack of steepness, this hypothesis cannot be supported. These contradictions are consistent with the limited importance of dominance rank in gorilla society and consistent with that of some other female transfer species. Within some primate groups, a high degree of inter-individual competition (often over food) is often indicative of a strong, linear dominance hierarchy (Isbell and Young, 2002; Koenig *et al.*, 2004; Wrangham, 1980). Among the Riverbanks gorilla females, competition for food resources was virtually non-existent and no steep dominance hierarchy resulted. What is more, unstable hierarchies, such as the ones yielded in the analyses of approach-withdrawal and grooming interactions, typically include several rank reversals (Isbell and Young, 2002). Blue monkeys (*Cercopithecus mitis*) are a female transfer species that exhibit frequent rank reversal and an unstable dominance hierarchy (Rowell, *et al.*, 1991). In both dominance matrices, reversals of rank were evident between the observation blocks. The absence of a stable linear hierarchy among the females illustrates the "egalitarian" nature of gorilla society (Harcourt and Stewart, 2007).

While there was no significant competition for food in the Riverbanks group, the females do have to compete for their one reproductive resource- the male. For a recently nubile female entering a secondary group, being able to

secure the attention of the silverback is key in ensuring her reproductive success. (Stokes, 2004; Watts, 1990) For this reason, a female entering a new group is often met with tension from the other females (Stokes, 2004). This could explain the high rate of solicitation of the adult male by both Macy and Kazi. Both females are newly sexually mature and focused on the male for their reproductive opportunities. Macy essentially outcompeted Kazi in terms of solicitations, winning the favor of the male. Interestingly, once Macy had Cenozo's favor, she began interacting much more consistently with Kazi and Acacia.

In addition, nonconceptive mating is a tactic that has been observed in captive western lowland gorilla females that is used to depleting the group male's sperm and lowering the chances that other females can conceive (Stoinski *et al.*, 2009). Vying for a male's attention appears to be an implicit method of competition that does not result in a rigid hierarchy. It is possible that nonconceptive mating may have played a role in the Riverbanks group and that reproductive competition is innate, regardless of its irrelevance in a zoo environment.

### **Stereotypical Behaviors**

One of the benefits of ethological studies on zoo animals is that it provides an appropriate environment in which to assess how the conditions of captivity affect animals. Thanks to the dedicated work of scientists and zoo staff alike, captive environments are now much more suitable for wild animals than they



have been in the past. Even so, the conditions of captivity still can alter certain aspects of animal behavior. Stereotypical behaviors are those that are repetitive and unvarying that lack a particular function to the animal. Animals that display stereotypic behaviors are often described as exhibiting "zoochosis" (Shyne, 2006). Redirecting behaviors through the implementation of innovative stimuli has been shown to reduce the occurrence of stereotypical behaviors in several species of zoo-housed animals (Hosey, 2005; Meder, 1992).

Captive gorillas have displayed several distinctive behaviors that are not found in wild populations, though not all of these behaviors have negative consequences (Meder, 1992). A perfect example of this is tandem walking. This behavior is commonly witnessed in captive gorillas and it adds another dimension to analyses of affiliation in captive western lowland gorilla groups. (Bennett and Fried, 1990; duBois *et al.*, 1991). Despite this, several stereotypical behaviors have been identified in captive gorilla populations and are believed to have deleterious effects (Bennett and Fried, 1991; duBois *et al.*, 1991; Hosey, 2005; Lukas, 1999). In my study group, the only stereotypical behaviors that were observed were head rolling and regurgitation and reingestion. The first of these behaviors, head rolling, involves repeated movements of the head, sometimes consecutively. The behavior is characterized as stereotypical in that the animal is not moving to look at something in its environment (Bennett and Fried, 1990; duBois *et al.*, 1991).

Only Acacia was observed to head roll, all of which took place in Block 1. She always performed this behavior when Cenzoo came into view. As evidenced by the rate of affiliation and agonism between Acacia and Cenzoo, they did not coexist harmoniously on a consistent basis. One obvious possibility is that head rolling was Acacia's response to an unwanted presence. Upon further investigation, I came to discover that Acacia's head rolling was more of a personal quirk than a serious sign of distress. She, along with her genetic relatives, all perform unusual behaviors, which include head rolling and ear-holding, on a somewhat consistent basis (Brian Goleman, Keeper of Gorillas/Small Mammals, and Emily Lopez Guertin, Senior Keeper of Gorillas/Small Mammals, personal communication). Because this behavior disappeared by the second block, I would conclude that Acacia's head rolling was not a sign of serious distress.

The other observed stereotypical behavior, regurgitation and reingestion (R/R), is the voluntary expulsion of digested food from the stomach and consumed again. This behavior has been seen in approximately 65 percent of captive gorillas and is attributed to a gorilla feeling a lack of control in its environment rather than to an upset stomach. Prolonged repetition of this behavior is suggested to cause serious damage to the esophagus and digestive tract (Lukas, 1999). While R/R has not been formally reported for wild populations of gorillas, the potential for its occurrence cannot be ruled out. Other primate species, such as bonnet macaques, often perform similar behaviors in the wild, which are not considered abnormal (Johnson *et al.*, 2007)

Kazi's stereotypical behavior, R/R, was most often witnessed in the early mornings before the group was allowed into their outdoor enclosure. Most of these R/R episodes occurred close together. For example, Kazi had three recorded days of R/R, with multiple instances of the behavior occurring on a given day, and usually within one or two 15-minute focal periods.

It has been suggested that R/R is a sign of distress in response to a different schedule, or one that does not provide food as frequently (Lukas, 1999). Since the Riverbanks gorillas had regular access to browse in addition to their scheduled meals, the latter is probably not the case. However, since Kazi arrived from Zoo Atlanta most closely to the initial group introduction, it is possible that she was still adjusting to the change of schedule. While the behavior still persisted in the second block, it only occurred on one out of the 17 days in that block. It is interesting that Macy, who arrived with Kazi, did not exhibit the same frequency of R/R. Macy's infrequent display of this behavior could be attributed to being otherwise occupied with Cenozo.

The decrease in the performance of stereotypical behaviors in the study group between blocks suggests that their occurrence was connected to acclimating to a new schedule, new surroundings, and new group members. This provides additional confirmation that the group members adjusted well in the initial months after introduction.

## **Conclusions, Questions for Further Research, and the Future of Gorillas**

Nuanced and varied behavioral strategies are at the root of an individual's intra-group and reproductive success. Adjusting one's rate of affiliation and agonism in dyadic interactions is just one of the ways great apes can be socially and reproductively successful in their groups. Increased affiliative interactions have been shown to benefit gorillas' reproductive success, particularly that of males (Harcourt and Stewart, 2007; Smuts and Smuts, 1993). In the study group, affiliative interactions increased in male-female dyads over time, which should lay the foundation for several reproductive opportunities in the future.

The needs of females are central to a primate species' group composition. Females' distributions are generally influenced by nutritional resources whereas males are influenced by the presence of reproductive resources (females) (Harcourt and Stewart, 2007; Stokes *et al.*, 2003; Stokes, 2004). Studies that investigate the behavioral patterns of females are critical when understanding more about a group's social organization in a species like the western lowland gorilla.

It is estimated that among prosimians, monkey, and apes, approximately three to ten percent of an animal's daily activity budget is used for social interactions. Primate social life is driven by competition and aggression, but more importantly, it is also driven by affiliation and cooperation (Sussman *et al.*, 2005). It is suggested that affiliative interactions are much more successful in forming alliances, obtaining access to mates and other resources, and maintaining a strong

social network. Coordinating one's actions with those of the individuals in their group ultimately promotes group cohesion.

Group cohesion is necessary when living in such constant, close proximity as is the case in captivity. In the wild, a tightly-knit group helps in each individual's survival by providing increased protection from predation and intergroup agonism (Harcourt and Stewart, 2007; Stokes, 2004). In the end, animals that focus on social strategies that promote group formation many more benefits than another animal who adopts individualistic strategies (Dunbar and Schultz, 2007).

In this study, females were mostly responsible for the higher rates of affiliative behaviors than agonistic ones. Also, the increase in affiliation (and decrease in agonism) over time promoted group cohesion and strengthened bonds, as evidenced by the females spending so much time with one another. This is an excellent indicator that the group will do well together in the long-term.

In the study group, there were more instances of grooming than withdrawal and the results of the grooming matrix appeared to be much more representative of the kind of intrasex relationships observed in the wild as well as in other captive groups of western lowland gorillas (Harcourt and Stewart, 2007; Robbins *et al.*, 2005; Scott and Lockard, 2007).

The analysis of intragroup and intrasex relationships can be validated by the kinds of relationships detailed in captive and field studies, which have noted a lack of consistent linearity among females evaluated by similar criteria (Scott and

Lockard, 1999; Watts, 1994). Moreover, in agreement with the work of Fischer and Nadler (1977) and Scott and Lockard (1999), body size, which characteristically increases with age, did not play a significant role in a female's social status within my study group.

While this project yielded some remarkable results, there is still much that could be studied with this particular group. With consideration of captive animal management, it would be informative to monitor how different types of enrichment affect the group members' interactions with one another. The Riverbanks keepers already do an excellent job of providing extra stimulation for the group. As it stands now, the group receives novel food (e.g. popcorn, raisin boards) and enclosure items (e.g. barrels, boomer balls) throughout the week, has access to two artificial termite mounds that are filled with food enrichment, and the male gets a special afternoon feeding. Monitoring the group's interactions after providing enrichment that exercises a different sense (e.g. smell, taste, touch) could allow keepers and staff to assess which items are best at promoting species-typical behaviors and curbing boredom. Boredom can become a problem in a captive setting, as the environment in which animals find themselves is not nearly as varied as they might encounter in the wild. If left without novel stimuli, captive animals' boredom could manifest into aggression or stereotypical behaviors (Hosey, 2005). With specific regard to Cenzoo, it is possible that certain types of environmental enrichment can better redirect his periodic aggression toward the females. So far, his additional feeding seems to do this

quite well. Furthermore, the addition of more nesting substrate in the outdoor enclosure could further reduce the already low number of supplants in dyadic interactions.

Another potential area of research involves intragroup interactions. Since the two half-sisters and the male have breeding recommendations, it would be highly informative to conduct a future study with the group to see if relationships change with the addition of one or more infants. Mother gorillas often encourage their infants to socialize with their peers as well as older individuals in the group (Maestriperi *et al.*, 2002). Furthermore, allomothering is common in gorillas and other female transfer species that lack strong dominance relationships (Fossey, 1979; McKenna, 1979; Nakamichi *et al.*, 2004). A logical prediction is that the instances of affiliation would increase even more with the presence of one or more infants.

The results of this project provide a better picture of the social repertoire of gorillas during an introductory period as well as further insight into the development of their social relationships in captivity, both of which suggest that the members of this group of western lowland gorillas have adjusted well to their new surroundings. This is partly thanks to the effective management strategies zoos have used to form an optimal family group, ensuring both physical and psychological health of the group members.

There may come a time where captive gorillas will contribute to the continued existence of the species in the wild, which is why understanding the

species' social dynamics in critical. Currently, scientists are working on reintroducing several other critically endangered species, like golden lion tamarins (Stoinski *et al.*, 2003), gibbons (Cheyne *et al.*, 2008), and Sumatran orangutans (Grundmann, 2006) to their natural habitats. Thus far, their work has shown that with some reinforcement of species-typical behaviors and acclimation to the natural environment, these individuals are capable of surviving on their own with a lack of provisioning by utilizing their complex ecological adaptations. Currently, displaced or orphaned gorillas are currently being rehabilitated and successfully reintroduced to the wild, but their numbers are still declining due to human activity (Courage *et al.*, 2001). The work of zoos in managing captive animals is becoming increasingly important, as species' numbers decline on a daily basis. Combined with conservation strategies in the field, zoos' efforts are paramount in the preservation of western lowland gorillas and other threatened wildlife.



**Appendix 1: Sample Data Collection Sheet**

**Riverbanks Gorilla Observations**

**Sheet:** \_\_\_\_\_

**Weather:** \_\_\_\_\_

**Date:** \_\_\_\_\_

**Focal Animal:** \_\_\_\_\_

**Start Time:** \_\_\_\_\_

**End Time:** \_\_\_\_\_

<b>Time</b>	<b>Behavior</b>	<b>Proximity</b>	<b>Notes</b>

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