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Introducing a Silverback to an Established Group of Adult Female Western Gorillas (Gorilla Gorilla Gorilla)

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INTRODUCING A SILVERBACK TO AN ESTABLISHED GROUP OF ADULT FEMALE GORILLAS (GORILLA GORILLA GORILLA)

A Thesis

by

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ABSTRACT

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In May of 2015, an attempt to introduce a new silverback (adult male) to an established group of six western lowland gorillas (*Gorilla gorilla gorilla*) housed at Gladys Porter Zoo failed. The introduction process was halted and only protected contact among the gorillas was allowed. On May 1, 2018 another introduction was initiated to three adult females. Twelve months of behavioral data were compared across three time periods and two environments. We predicted that an increase in agonistic and affiliative behaviors would occur while anxious behaviors would decrease. We observed a significant increase in affiliative behavior and a significant decrease in anxious behavior outdoors. Significant decreases in locomotion, manipulation and stationary behaviors were also observed. In contrast to other reports, levels of agonism were low in all conditions. This second introduction attempt is judged successful. The prolonged period of protected contact and reduced group size may have facilitated group formation.

DEDICATION

The completion of my master studies would not have been possible without the love and support of my family. My husband, Heriberto Cuellar III, my son, Rowan, my mother, Vicenta Martinez, my father, Pedro Martinez II, and my sister, Lillian Jaramillo, wholeheartedly inspired, motivated and supported me by all means to accomplish this degree. Thank you for your love, guidance and patience. Your kindness will never be forgotten.

It is also dedicated to the gorillas at the Gladys Porter Zoo who have captured my heart and taught me to stop and watch the world around me more.

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CHAPTER I

INTRODUCTION

In 2013, the western lowland gorilla exhibit at Gladys Porter Zoo (GPZ) consisted of seven gorillas. The family group included one adult male, known as the silverback, three adult females, two adolescent females and one juvenile male. In addition to the family group, three other silverbacks were present but were separated from the family group. The silverback of the family group, named Moja, had been acquired by GPZ on July 3, 1997 from Miami Metrozoo (see Figure 1). His family group, at the time of his arrival, was made up of 2 adult females and 2 adolescent females; these females were all full sisters. As time passed one of the females was transferred to another zoo on a breeding loan and another passed away. In 2011 a new adult female was introduced to the family group. During his time at GPZ, Moja sired 14 offspring from the 5 different females.

Figure 1: Moja. Gladys Porter Zoo's former silverback.

On April 15, 2013, Moja, 29 years old at the time, died unexpectedly from cardiovascular disease. His presence at GPZ marked the "glory days" of the gorilla group at the time, and his long time success as the silverback produced the "established group" upon which this study focused on.

Statement of the Problem

Following Moja's death, the zoo's surviving group was left without a silverback for 2 years and the social structure of the group disintegrated. The increase in solitary behavior and decrease in social behavior suggested that the GPZ gorillas experienced some behavioral disruptions associated with Moja's death (James-Aldridge & Martinez, 2016). In late 2014 a new silverback was acquired, but an attempt to introduce him to the group was judged a failure, and a decision was made to retreat to earlier stages of the introduction process, allowing protected contact only between the male and his prospective new family group. A second attempt at a full introduction was initiated on May 1, 2018 and provides the focus of this thesis.

Statement of the Purpose

In this study I investigate how the introduction of a new silverback gorilla affected the behavior of the already established family group of western lowland gorillas (*Gorilla gorilla gorilla*) housed at the GPZ in Brownsville, Texas. Additionally, I briefly examine the variables that may have differed between the recent successful introduction and the unsuccessful attempt in 2015. The purpose of the study is to provide a better understanding of the role a silverback plays within his family group. In conclusion, understanding the behavioral responses of group members to changes in group structure can better prepare zookeepers to plan their management strategy when periods of social change are unavoidable.

CHAPTER II

REVIEW OF LITERATURE

Biological Relationship Between Humans and Primates

A primate is a member of the group of mammals that include lorises, tarsiers, lemurs, monkeys, apes, and humans. Primates are highly complex and intelligent animals. They possess features like forward facing eyes, thumbs with the ability to grasp, and enlarged brains with increased areas that emphasize seeing over smell (Falk, 2000). Humans have found these shared common features to be especially interesting. Thus, the study of nonhuman primates, known as primatology, began.

Primatology provides an opportunity for humans to learn more about their basic primate natures and it helps scientists better understand the course of human evolution. The comparison of genomes among apes and humans can help explore the origins of humans and when the separation from the great ape species occurred. Humans are genetically more related to apes than any other animal on earth. Although the closest nonhuman primate relative to humans is generally believed to be the chimpanzee (*Pan troglodytes*) (Ellegren, 2005; Goodman, 1999; Khaitovich et al., 2005; Waterson, Lander, & Wilson, 2005), a recent study has suggested the human genome more closely resembles the gorilla genome than they do the chimpanzee genome (Scally et al., 2012). Even though we, as humans, are closely related to the great apes we did not directly evolve from them. Humans and chimpanzees, for example, shared a common ancestor that lived millions of years ago. Many scientists believe that the evolutionary split occurred between 5 million and 6 million years ago (Falk, 2000).

Gorillas in their Natural Habitat

Taxonomy

Gorillas are one of the five genera that make up the ape family, the others being the gibbons, orangutans, chimpanzees and humans, and are the largest living primate of all. A recent taxonomic reclassification has now grouped gorillas into two species and four subspecies (Groves, 2001). Western gorillas include western lowland gorilla (*Gorilla gorilla gorilla)* and cross river gorilla (*G. g. diehli*). Eastern gorillas include eastern lowland gorilla (*G. g. graueri)* and mountain gorilla (*G. g. beringei)*.

Morphology

Butynski (2001) found that western and eastern gorillas are more genetically distant from one another compared to their primate relatives, the chimpanzees (Pan troglodytes) and bonobos (Pan paniscus). Along with this genetic distance there are physical differences between subspecies of gorilla that reveal individual morphological characteristics as well (Rowe 1996; Leigh et al. 2003). Western lowland gorillas have brownish gray coats and are smaller than the other subspecies of gorillas. Cross river gorillas share the same appearance as western lowland gorillas, but have a wider skull and smaller ears. Mountain gorillas have brownish gray coats that are longer and thicker than their conspecifics. Eastern lowland gorillas have long faces and have black coats that are shorter than their subspecies' cousin, the mountain gorilla.

All subspecies of gorillas exhibit pronounced sexual dimorphism. Males become silverbacks around the age of 14, exhibiting silver hair across their shoulders and down their back. Other secondary sex characteristics include having large crests on their heads, large canines and being double the size of adult females. Males can weigh up to 181 kg and in their natural habitat and 227 kg in human care and measure 1700 mm in height, while females can weigh up to 72 kg in their natural habitat and 98 kg in human care and measure approximately 1500 mm in height (Rowe, 1996).

Gorillas spend most of their time on the ground and walk while supporting their weight on their knuckles. Although gorillas are mainly terrestrial, young gorillas frequently move around and play in trees. All subspecies of gorillas engage in a limited amount of bipedal standing. This form of locomotion appears especially often when gorillas perform chest-beating displays (Falk, 2000). Finally, the lifespan of gorillas in the wild can range from 30 to 40 years (Hoff, Hoff, and Maple, 1998).

Habitat

In the wild, western and eastern gorillas live in dramatically different habitats due to being separated by the 1,000 km of the Congo Basin forest in Africa. Western lowland gorilla habitats can be found in parts of Nigeria to the western edge of the Democratic Republic of the Congo, eastern lowland gorillas live in the eastern part of the Democratic Republic of the Congo and mountain gorillas live in tiny enclaves at high altitudes in Uganda, Rwanda and the Democratic Republic of the Congo (Falk, 2000). Cross river gorillas inhabit the lowland montane forests and rainforests of Cameroon and Nigeria (Etiendem, Funwi-gabga, Tagg, Hens and Indah, 2013).

Social Organization and Behavior

The average group size of gorillas consists of 10 individuals (Harcourt & Stewart, 2007; Parnell, 2002). These groups usually contain one silverback, numerous adult females, and their offspring. Terms used to describe the age and sex classification of gorillas include: *infants* who are less than 3 years of age, *juveniles* who are between 3 to 6 years of age, *adolescents* who are between 6 to 8 years of age, *adult females* who are more than 8 years of age, *blackbacks,* males between 8 to 13 years of age and *silverbacks* who are 14 years of age or older (Robbins, 1999).

Adult females are usually not related to one another due to female gorillas transferring from their natal group to new groups once reaching maturity (Harcourt, Stewart, & Fossey, 1976; Stewart & Harcourt, 1987). Female gorillas have their own dominance hierarchy among each other (Watts, 1994). The hierarchy is usually based on characteristics of each individual female, such as the timing of when they joined the group, age, and fighting ability (Van Schaik, 1989; Scott & Lockard, 1999). Therefore, the females with the longest tenure/age are the highest ranking (Stewart & Harcourt, 1987; Watts, 1985, 1991a). Male gorillas, like the females, also emigrate from their natal groups once they reach maturity. However, males usually tend to remain alone until they attract females (Harcourt et al., 1976). Males must attract females in order to form new breeding groups (Maple & Hoff, 1982).

Adult females and other members of the group rely heavily on their silverback. The silverback's role is to protect the group from danger, mediate intragroup aggression, and maintain the social structure of the group (Hoff, Nadler, & Maple, 1982). The silverback protects his offspring from being killed by other males and protects the group from predators such as large cats and humans (Harcourt & Stewart, 2007). When conflicts between females arise the silverback intervenes aggressively to end them (Harcourt 1979a; Watts, 1991b). In the wild most adult females are unrelated, thus the bonds among themselves are weak or nonexistent and consequently group structure is formed because of the affiliation between the silverback and each of these adult females (Maple & Hoff, 1982). Gorilla family groups are long-term which helps to strengthen group structure and create stable relations between the dominant silverback and the adult females (Fossey, 1979; Harcourt, 1979; Yamagiwa, 1983). These bonds are also strengthened by the birth of infants (Yamagiwa, 1983).

In the wild when a silverback passes away three scenarios may occur: a male from within the group may take over, a new silverback may come along and take over, or the remaining group members disperse (Hoff *et al*., 1982). As noted below, these options are not available to gorillas in human care.

Gorillas in Human Care

The welfare of nonhuman primates in zoological institutions has greatly improved over the years. Zoo researchers have learned to improve the daily lives of animals in human care by identifying and providing environmental stimuli essential for optimal psychological and physiological health, called environmental enrichment (Shepherdson, 1998). An emphasis is also placed on the importance of providing appropriate enrichment to the specific biology of the species under consideration (Mellen and MacPhee, 2001). For example, Charmoy and Miller (2015) found that automatic belt feeders that could feed at randomized times increased the amount of time their zoo-housed gorillas spent looking for, obtaining, and eating food. Thus, the increased amount of time foraging, increased the gorillas overall activity levels and altered their behavior towards a more naturalistic direction.

The zoo community is always willing to learn new ways to improve the lives of the animals in their care. Swaisgood and Shepherdson (2005) conducted a meta-analysis on enrichment in zoos and found that 53% of the studies included showed that zoo researchers tackle stereotypic behaviors with diverse and inventive enrichment strategies that resulted in a significant reduction of stereotypy performed. Zoo institutions try their best to prepare and create strategy plans for all kinds of situations that can affect the animals. Yet, certain events seldom occur that little to no literature is written about it. One of these events is the death of silverbacks in human care. The death of a silverback has been a rare occurrence in zoos since gorillas usually live to be over 40 to 50 years in human care. Therefore, only a handful of zoos have studied the phenomena and even then only a few of those have also been able to study the effects of introducing a new male to the remaining group.

Johnstone-Scott (1998) observed a family group of western lowland gorillas at the Jersey Wildlife Preservation Trust who were introduced to a new male following the death of their founder male, Jambo. After Jambo passed away the remaining group consisted of four mature females, two female offspring and an infant male. Following the loss of Jambo, the family group experienced a partial breakdown in its social structure, as evidenced by the frequent bouts of unruly behavior by the younger females. The harassment of the lowest ranking female Julia, the eldest female N'Pongo and her infant Asato became a frequent occurrence. When the new male, Ya Kwanza, was initially introduced there was an increase in affiliative behavior among the adult females. This was especially evident in the dominant female, Kishka, who would rarely leave the side of another adult female who had an infant that was sired by Jambo. Lastly, an increase in agonism was also observed. One of these instances of agonism happened during a disagreement between several of the females over forage. Ya Kwanza charged the troop and in the process, an adult female named Julia was clearly targeted and bitten by the silverback on her shoulders and thighs. However, even though the introduction of Ya Kwanza was problematic at first, there was a decrease in anxious behavior over a period of about 6 months and thus leading to a siring of a male infant from the youngest female.

Hoff, Hoff, and Maple (1998) observed the behavioral responses of a family group following the silverback, Rann's, death in Zoo Atlanta. Based on a previous study, in which the silverback had been removed from the social group (Hoff *et al.,* 1982), Hoff *et al.* (1998) hypothesized an increase in aggressive behaviors and mother-offspring relationship. In their study the remaining group members consisted of two adult females and two juvenile males. After Rann's death there was, as hypothesized, a significant increase in aggressive behaviors, such as lunge, displace, quadrupedal stiff stance and head divert behaviors. The mother-offspring pair relationship intensified as well.

Margulis, Whitham, and Ogorzalek (2002) studied a family group at the Brookfields Zoo, that had recently lost their silverback, Chicory. The remaining group was left without a silverback for about 3 months and during this time the researchers found an increased level of agonism among the 4 adult females. Margulis *et al.* (2002) hypothesized that the absence of the silverback and the subsequent introduction of a new male would influence female-female interactions. Moreover, after the new male was introduced aggressive behaviors were predicted to decrease over time while social affiliative behaviors among females would increase. They found that aggression remained high for several months but decreased gradually after the new male, Ramar, was introduced. Finally, social affiliative behaviors increased for all females, which suggests that the silverback presence brought stability to the group. This stability then enables females to engage in social affiliative behavior and reduce aggressive behavior. Margulis *et al.* (2002) suggest the individual differences among silverbacks can play an important role in how long it takes for males to take control of their new group.

Less, Lukas, Kuhar and Stonski (2010) studied a multi-male, mixed-sex group at the Pittsburgh Zoo and Pittsburgh Plate Glass (PPG) Aquarium following the death of the silverback, Mimbo. They predicted that agonistic behaviors would increase after the death due to social stability change. They observed an increase in displacements among the group. Furthermore, feeding decreased and there was an increase in self-directed behaviors (e.g., self-grooming and scratching) post-death. A difference in spatial distance among individuals was also observed, with group members becoming more dispersed.

Finally, Weerd, Knotters, & Brink (2010) observed the Artis Royal Zoo gorillas, who had recently lost three of its members, the silverback, a blackback male and an adult female, to an infection. The females who survived had problems dealing with the loss, which was shown by their poor eating habits and lack of activity. Hence, a new silverback named Kumba was introduced to the two surviving females. The data indicated there were significant changes in behavior for both females. Weerd *et al.* observed significant decreases in locomotion and stereotypic behavior after the introduction. Moreover they observed a significant decrease in interaction with the public in one of the two females. However, in contrast to previous studies aggressive behavior did not increase when Kumba was introduced nor was there an increase in affiliative behavior between the two females.

In addition to the limited number of studies on the behavior of a group following the death of its silverback in human care, a few studies in which a silverback was removed from the social group or group membership was modified do exist. Hoff *et al.*, (1982) conducted their study at Yerkes Regional Primate Research Center and removed the silverback from a group of gorillas in human care to examine its control role in the group. Hoff *et al*, study took place in Zoo Atlanta and group membership was modified as an ongoing study of the management processes concerning gorillas. Both these studies observed an increase in aggressive behavior among the remaining group members (Hoff *et al*., 1982, 1996). Hoff *et al*., (1982) also observed an increase in mother-infant social behavior when the silverback was removed and an increase in proximity between the females and a decrease in stationary behaviors. When the silverback was returned there was an immediate rise in aggression from the male and a decline in female aggression, which gradually returned to baseline levels. Similarly, Hoff *et al*., (1996) observed an increase in contact between the remaining group members and a decrease in resting after the group membership was changed. These researchers also observed an increase in eating after the introductions.

When primates in human care pass away or are introduced to a new setting, humans try to anticipate the responses these animals may have based upon the close relationships they have developed with the animals they work with. These relationships, however, may give zoo personnel a false expectation of how each animal will react to these sudden changes. To better prepare for unavoidable situations zoo personnel should also consult on reviewed literature to help make the process smoother for the animals.

CHAPTER III

FIRST INTRODUCTION ATTEMPT

Mbundi's History

With Moja's sudden passing and the breakdown of the family group's social interaction, the zoo knew they had to find a new silverback to take his place. When Association of Zoos and Aquariums (AZA) accredited zoos submit a request that a new animal to be transferred to their facility, the request is reviewed, and if approved, the AZA's Species Survival Plan (SSP) will recommend a specific animal. The SSP is a population management and conservation program whose goal is to maintain a variety of animal populations in human care that are both genetically diverse and demographically stable (Association of Zoos and Aquariums, 2020).

When the GPZ requested a new silverback the SSP recommended the transfer of a then 21-year-old, male named Mbundi (see Figure 2), from the Kansas City Zoo. Mbundi was born at the Calgary Zoo and was raised by his mother Tabitha. He was transferred to the Kansas City Zoo along with his half-brother N'tondo in 1999 and they were placed in a bachelor group. The brothers had initially been housed with an older male named Radi, but upon reaching adolescence they were becoming too aggressive with the older male and were separated from him in 2005.

Mbundi was selected as the SSP recommendation based upon his reproductive history (had never sired offspring and was, thus, not yet represented in the gene pool) and temperament. The Kansas City Zoo described Mbundi as a somewhat laid back but observant gorilla. They stated that he was very aware of his surroundings and would keep a close eye on keepers and other gorillas in the building. Despite being described as an observer, Kansas City zookeepers reported that he would not solicit attention or items from keeper staff (Kansas City Zoo, 2014). Further, although he lived in a bachelor group himself, Mbundi was exposed to female gorillas that were housed in a family group in the same enclosure at the Kansas City Zoo. During that time he had shown more interest in the female gorillas (i.e., where they were and what they were doing) and when the females were on exhibit he would walk/pace around the off-exhibit living spaces trying to look for them and vocalizing to them. Mbundi was also known to display towards the females often (Kansas City Zoo, 2014).

Figure 2: Mbundi. Gladys Porter Zoo's new silverback. Photo taken by Tony Chavez, 2-Tone Photography, LLC.

Introduction Timeline

A year and a half after Moja's death, Mbundi arrived at GPZ on November 19, 2014 (See Appendix B for detailed timeline). After his six-week quarantine period, on January 29, 2015, he was moved to the gorilla enclosure to off-exhibit living space number 8, a location that allowed all the gorillas to have *nontactile* sensory contact with one another (i.e., the gorillas could see, smell, and hear, but not touch, one another) (See Appendix A for gorilla exhibit layout). Once the gorillas were accustomed with each other through sensory contact, Mbundi was moved to off-exhibit living space number 2 on March 19,2015. This move allowed protected contact between Mbundi and the other gorillas (i.e., they were able to touch one another through a mesh barrier).

After a month of protected contact among the gorillas, Mbundi was allowed full access to the group inside the building on April 14, 2015. The group was allowed to be together in the outdoor exhibit for the first time on April 23, 2015. All seemed to be progressing well until May 3, 2015, when Mbundi was observed biting one of the adult females named Kiazi. Two days later he was observed fighting with another adult female named Penney. Then on May 7, 2015, T.J., a young juvenile male, was removed from the group when it was discovered that he had received a wound in his pelvic area. Then on or about May 14, 2015, an adolescent female named Margaret was found with a severe wound to her left arm. Given the number and intensity of these aggressive encounters, it was decided to remove Mbundi from the family group. Consequently, Mbundi's socialization process was halted.

CHAPTER IV

SECOND INTRODUCTION ATTEMPT

The 2015 attempt to introduce the newly arrived silverback, Mbundi, was judged a failure, and a decision was made to retreat to earlier stages of the socialization process, allowing protected contact only between Mbundi and his intended group. A second attempt at a full introduction was initiated on May 1, 2018.

In this chapter I present the results of an analysis of the gorilla group's behavior over the course of the year 2018, the year in which the second introduction of Mbundi to a potential family group took place. To conduct the analysis, I divided the calendar year into three segments; the first from January through April, i.e., the four months preceding Mbundi's full contact with the group; the second from May through August, i.e., the four months immediately following that initial full contact; and the third from September through December, i.e., the four months constituting a more extended period of group familiarity, to facilitate an examination of possible changes in group behavior over time.

Subjects

Mbundi's first attempted introduction in 2015 was to a group of six gorillas, comprised of five adult females and one juvenile male. During the interim between the first and second introduction attempts, the size of Mbundi's intended group declined from six to three after two of the animals, one adult female and the juvenile male, were moved to a different group (and, ultimately, to different zoos) and the death of one of the adult females. The resulting, smaller group was, thus, comprised of three adult females by 2018 (See Appendix D. for a detailed description of the gorillas).

Observational data were retrieved from the Gladys Porter Zoo's Behavior Database for the four gorillas forming the focus of the present study: adult silverback, Mbundi, male, age 25 years (See Figure 3); and three adult females, Penney, age 32 years (See Figure 4), Martha, age 29 years (See Figure 5), and Margaret, age 11 years (See Figure 6). Penney and Martha are full sisters. Martha and Margaret are mother and daughter, with Margaret having been sired by the former silverback, Moja. All three females were of reproductive age, and two of the three were multiparous. Penney had given birth to two infants previously, Martha to five. Margaret was nulliparous. All three females were administered oral combination birth control tablets (Sprintec; norgestimate and ethinyl estradiol, 0.250 mg and 0.035 mg) until July 18, 2018, however, at which point zoo staff felt comfortable releasing them from the contraceptive.

Figure 3: Mbundi. Adult silverback.

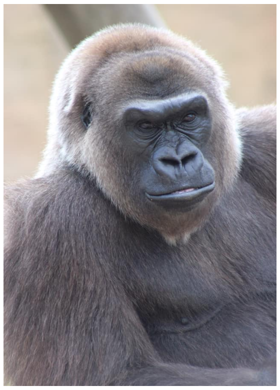

Figure 4: Penney. Adult female.

Figure 5: Martha. Adult female.

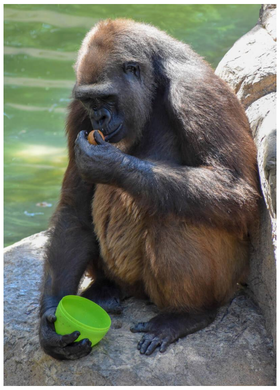

Figure 6: Margaret. Adult female.

This study was approved by the Institutional Animal Care and Use Committee of the University of Texas Rio Grande Valley and by the Animal Care and Use Committee of the Gladys Porter Zoo.

Study Site

The gorillas were housed at GPZ, located in Brownsville, Texas, in three different enclosures depending on the time of day and/or weather conditions. These included: an outdoor exhibit area comprised of an "island" surrounded on three sides by a shallow water-filled moat that the gorillas could easily access (See Figure 7), palm trees, grass, and a three story climbing area; a large indoor enclosure fronted by large windows allowing public viewing, furnished with artificial large rocks and ledges and provisioned with hay; and a series of off-exhibit living spaces that are not visible to the public (See Appendix A. for a schematic diagram of the gorilla exhibit).

The Gladys Porter Zoo is accredited by the Association of Zoos and Aquariums.

Figure 7: The Island. The outdoor gorilla exhibit area.

Procedure

Twelve months of archived behavioral data were collected from the Gladys Porter Zoo's Behavior Research database for each of the four study subjects. All data had been collected by means of focal animal sampling (Altmann, 1974) by either the zoo's Curator of Behavior Research or by trained assistants as part of the zoo's routine monitoring of gorilla behavior.

A total of 148 hours of behavioral data were collected based on an ethogram of 27 basic behavior codes (Appendix C). In this 12-month period, 51 observations hours took place before the introduction, 65 observation hours took place after the initial introduction, and 32 observation hours took place four months after the initial introduction. Due to observation hours not being evenly distributed over the time periods there may be a possibility of bias in my data collection approach.

Basic behaviors thought to be of interest to the present study were grouped into eight larger behavior categories: affiliative, agonistic, tension/anxiety, undesirable, locomotive, manipulative, stationary, and other behaviors (Table 1). Behavior categories were then compared across three time periods, and were examined separately for two environments, indoors and outdoors. The three time periods were designated as Period 1: *before full contact* with the new silverback (January-April, 2018), Period 2: *early full contact* with the new silverback (May-August, 2018), and Period 3: *later full contact* with the new silverback (September-December, 2018).

Table 1

Detailed Behavior Categories

Category	Behaviors Included
Affiliative	Contact Close (CC) and Contact Touch (CT)
Agonistic	Contact Touch- Aggressive (CTA), Display (D), Displace (Dsp), Respond to Displace (RD)
Anxious	AutoGroom (AuG), Hair Pull-Autogroom (HPA), Hair Pull (HP), Scratch (Scr), Submit/greet (Sub)
Undesirable	Coprophagy (Cop) and Regurgitation/Reingestion (RR)
Locomotion	Locomotion (L)
Manipulation	Manipulate (M)
Stationary	Stationary (S)
Other	Other (Oth.) (e.g., Copulation and/or intense aggressive attacks)

Method of Analysis

A two-way factorial ANOVA (3X2) was used. The first factor used was a within subjects factor: Time period. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The second factor used was a within subjects factor: Environment. The environment factor had two levels (inside and outside). All null hypotheses were tested using the *f-distribution,* at an alpha level of .10. This alpha level was selected due to the exploratory nature of the study and the small sample size. A higher alpha level would give the analysis more power to find significance in a small sample size.

Dependent Variables

Eight dependent variables were utilized in this study.

1. **Total Duration of Affiliative Behavior**

Total duration of affiliative behavior was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as affiliative behaviors. Affiliative behaviors were defined as the focal subject performing behaviors such as contact close and/or contact touch. Contact close was defined as the focal subject being 1 meter from another subject yet they are not touching one another. Contact touch was defined as the focal subject touching or being touched by another subject. See Figure 8 for an example of affiliative behavior.

Figure 8: Affiliative Behavior. Mbundi, Margaret and Penney foraging close to one another.

2. **Total Duration of Agonistic Behavior**

Total duration of agonistic behavior was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as agonistic behaviors. Agonistic behaviors were defined as the focal subject performing any of the following: contact touch aggression, display, displace and/or reaction to display. Contact touch aggression was defined as the focal subject touching or being touched by another subject in a manner that is rough or intense. Display was defined as the focal subject performing any of the following behaviors: upright stance, swaggering, running (bipedally or quadrupedally), chest beating, ground slaps and/or door pounding. Displace was defined as one individual approaching another causing the second to move away from his/her present position, which is then occupied by the first. Reaction to display was defined as the individual interrupting ongoing activity and orienting toward display being performed by another individual. See Figure 9 for an example of agonistic behavior.

Figure 9: Agonistic Behavior. Mbundi, Penney and Martha fighting.

3. **Total Duration of Anxious Behavior**

Total duration of anxious behavior was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as anxious behaviors. Anxious behaviors were defined as the focal subject performing any of the following: AutoGroom, hair pull, hair pull-AutoGroom, scratch and/or submit/greet. AutoGroom was defined as the focal subject self-grooming. Hair pull was defined as one subject plucking individual hairs from the subject being "groomed, frequently with the teeth. Hair pull-AutoGroom was defined as a self-directed version of hair pulling. Scratch was defined as rough, long scratches of the subject's own body that produced a distinct rasping sound, frequently diagonally across the torso or up nearly the entire length of an arm. Submit/greet was defined as an individual behaves in a manner that acknowledges the higher social status of another subject by performing any of the following toward the subject: bared teeth face, bared teeth scream, bob, crouch, back-up, flee, pant grunt, or present. See Figure 10 for an example of anxious behavior.

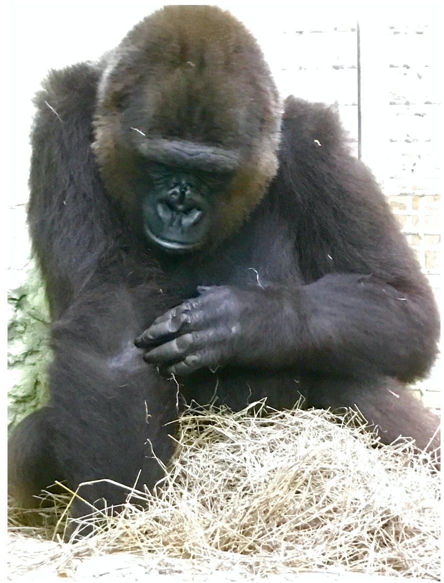

Figure 10: Anxious Behavior. Martha grooming her arm.

4. **Total Duration of Undesirable Behavior**

Total duration of undesirable behavior was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as undesirable behaviors. Undesirable behaviors were defined as the focal subject performing coprophagy and/or regurgitation/reingestion. Coprophagy was defined as eating one’s own feces or drinking one’s own urine, or consuming wastes that have been immediately captured from another. Regurgitation/Reingestion was defined as the focal subject regurgitating small amount of vomitus and reingesting it. See Figure 11 for an example of undesirable behavior.

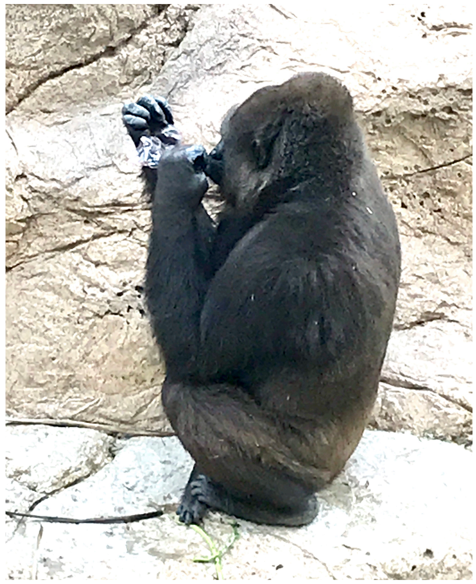

Figure 11: Undesirable Behavior. Martha in an example of regurgitation/reingestion.

5. **Total Duration of Locomotion**

Total duration of locomotion was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as locomotion. Locomotion was defined as the individual changing location by any active means by at least one body length; for example, walking, running, climbing, pirouetting and/or dangling by one arm. See Figure 12 for an example of locomotion.

Figure 12: Locomotion. Mbundi walking. Photo taken by Tony Chavez, 2 Tone Photography, LLC.

6. **Total Duration of Manipulation**

Total duration of manipulation was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as manipulation. Manipulation was defined as the individual closely investigating some physical object/s (may include body parts), handling it/them in some way. See Figure 13 for an example of manipulation.

Figure 13: Manipulation. Margaret manipulating a keeper provided basket.

7. **Total Duration of Stationary Behavior**

Total duration of stationary behavior was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as stationary behaviors. Stationary behaviors were defined as the focal subject being passive and not performing any of the other scoreable behaviors. This usually consisted of lying down, sitting, or standing while alone. See Figure 14 for an example of stationary behavior.

Figure 14: Stationary Behavior. Mbundi sitting alone. Photo taken by Tony Chavez, 2 Tone Photography, LLC.

8. **Total Duration of Other Behavior**

Total duration of other behavior was defined as the total amount of time (in minutes) subjects spent engaging in behaviors categorized as other behaviors. Other behaviors were defined as focal subject performing a behavior not described in the ethogram (e.g., copulation or severe attack). See Figure 15 for an example of other behavior.

Figure 15: Other Behavior. Mbundi and Margaret copulating.

Null Hypotheses

Each two-way ANOVA (3X2) tested six null hypotheses. The first three null hypotheses tested corresponded to main effects of factors Time period and Environment. The second three null hypotheses correspond to the first order, or two-way interactions between the factors. That is the interaction between Time period and Environment. Each of these six null hypotheses was used eight times, for a total of forty-eight hypothesis tested by this study. All null hypotheses were directional.

Results

Results are presented in eight sections, one section for each dependent variable measured: total duration of affiliative behavior, total duration of agonistic behavior, total duration of anxious behavior, total duration of undesirable behavior, total duration of locomotion, total duration of manipulation, total duration of stationary behavior, and total duration of other behavior.

Total Duration of Affiliative Behavior

A two-way factorial ANOVA (3X2) was conducted with total duration of affiliative behavior as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research questions of interest. All null hypotheses were tested at an alpha level of .10. Table 2 shows the results of the analyses.

Table 2

Total Duration of Affiliative Behavior ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	F	η_P^2
Within subjects					
Period	4,645	2	2,323	5.97**	.665
Environment	1.04	1	1.04	.040	.013
Period X Environment	27,824	2	13,912	7.93**	.725
"error" w1 (Period)	2,336	6	389		
"error" w2 (Environment)	77.8	3	25.9		
"error" w3 (Period X Environment)	10,532	6	1755		
Total	45,415.85				

Note. η_P^2 = Partial eta squared. *$p < .10$, **$p < .05$

There was a difference in total duration of affiliative behaviors among period 1 (M = 55.2 min., SD = 35.3), period 2 (M = 80.3 min., SD = 47.8), and period 3 (M = 47.7 min., SD = 36.5), $F(2,6) = 5.97$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .665$. There was no difference, however, in total duration of affiliative behaviors between inside (M = 60.9 min., SD = 38.5) and outside (M = 61.3 min., SD = 38.8) environments, $F(1,3) = 0.04$, $p > .10$. Finally, there was a significant interaction between the time periods and the environments, $F(2,6) = 7.93$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .725$.

Bonferroni pairwise comparisons were conducted to locate individual differences in total duration of affiliative behavior among the time periods. Table 3 shows the results of the analyses.

Table 3

Total Duration of Affiliative Behavior: Period Bonferroni Pairwise Comparisons

Period	Mean	1: Before Full Contact 55.2	2: Early Full Contact 80.3	3: Later Full Contact 47.7
1: Before Full Contact	55.2		NS	NS
2: Early Full Contact	80.3			NS
3. Later Full Contact	47.7			

Note. NS = not significant. $^{*}p < .10$, $^{**}p < .05$

The statistical power was not sufficient enough to detect a difference in total duration of affiliative behavior among time periods in pairwise comparisons, although the omnibus ANOVA was significant.

Two simple effects tests were conducted to explore the nature of the interaction effects between time period and environment on affiliative behavior. Table 4 shows the results of the first simple effects test.

Table 4

Total Duration of Affiliative Behavior: Period X Environment Simple Effects Test One: Differences Between Environments Within Time Periods

Period	*F*	Hypothesis df	Error df	Sig.
1: Before Full Contact	5.13	1.00	3.00	.108
2: Early Full Contact	10.1	1.00	3.00	.050**
3: Later Full Contact	5.80	1.00	3.00	.095*

Note. $^{*}p < .10$, $^{**}p < .05$

There was no difference in duration of affiliative behavior between environments observed during time period 1: Before Full Contact, F (2,2,) = 5.13, $p > .10$. There was a difference in duration of affiliative behavior, however, between In (M = 33.5 min., SD = 22.3) and Out (M = 127 min., SD = 76.1) environments during time period 2: Early Full Contact, F (2,2) = 10.1, $p < .10$. There was also a difference in duration of affiliative behavior between In (M = 81.4 min., SD = 64.3) and Out (M = 14.1 min., SD = 9.38) environments during time period

3: Later Full Contact, $F(2,2) = 5.80$, $p < .10$. Table 5 shows the results of the second simple effects test.

Table 5

Total Duration of Affiliative Behavior: Period X Environment Simple Effects Test Two: Differences Among Time Periods Within Environments

Environment	*F*	Hypothesis df	Error df	Sig.
In	3.99	2.00	2.00	.200
Out	43.0	2.00	2.00	.023**

Note. $*p < .10$, $**p < .05$

There was no difference in duration of affiliative behavior among time periods observed within the inside environment, $F(2,2) = 3.99$, $p > .10$. There was a difference, however, in duration of affiliative behavior among time periods observed within the outside environment, $F(2,2) = 42.98$, $p < .10$.

Bonferroni pairwise comparisons were conducted to locate individual differences among time periods in the outside environment. Table 6 shows the results of the analyses.

Table 6

Total Duration of Affiliative Behavior: Outside Environment Bonferroni Pairwise Comparisons

Env.	Period		1: Before Full Contact	2: Early Full Contact	3: Later Full Contact
		Mean	42.7	127	14.1
Out	1: Before Full Contact	42.7		**	NS
	2: Early Full Contact	127			NS
	3. Later Full Contact	14.1			

Note. NS = not significant. $*p < .10$, $**p < .05$

There was a difference in duration of affiliative behaviors between period 1 in the outside environment ($M = 42.7$ min., $SD = 31.1$) and period 2 in the outside environment ($M = 127$ min., $SD = 76.1$), $p < .10$. There was no difference, however, in duration of affiliative behaviors between period 1 in the outside environment ($M = 42.7$ min., $SD = 31.1$) and period 3 in the outside environment (*M* = 14.1 min., *SD* = 9.38), $p > .10$. There was also no difference in duration of affiliative behaviors between period 2 in the outside environment (*M* = 127 min., *SD* = 76.1) and period 3 in the outside environment (*M* = 14.1 min., *SD* = 9.38), $p > .10$ (See Figure 16).

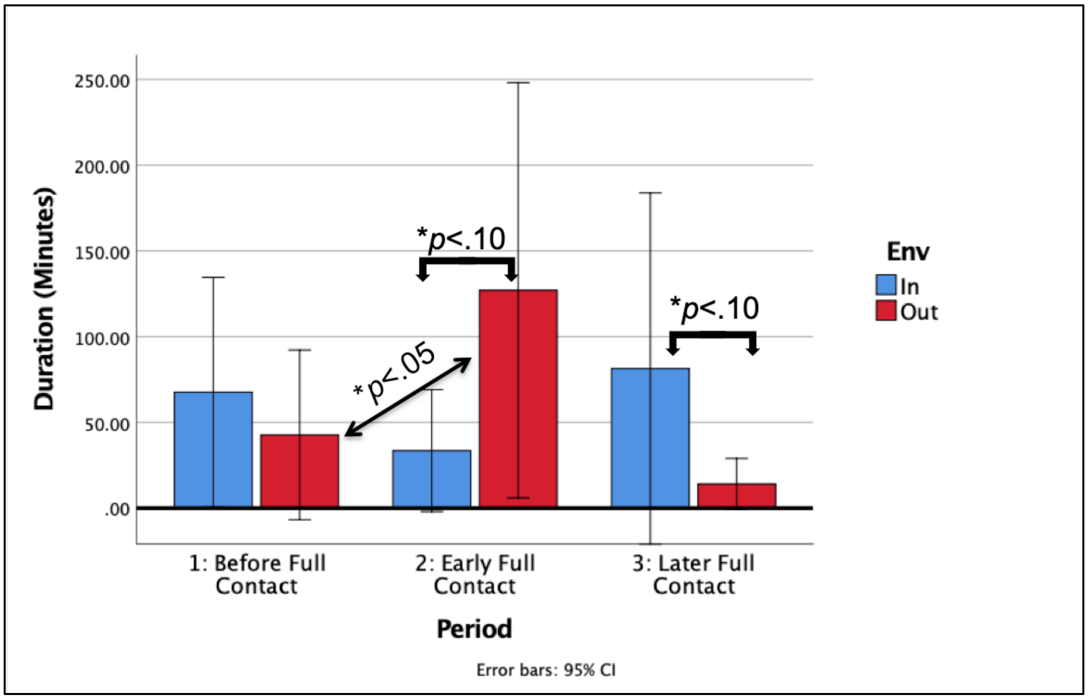

Figure 16. Affiliative Behavior Graph. Interaction effect of time period and environment on total duration of affiliative behavior. Standard errors are represented in the figure by the error bars attached to each column.

Total Duration of Agonistic Behavior

A two-way factorial ANOVA (3X2) was conducted with total duration of agonistic behavior as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research question of interest. All null hypotheses were tested at an alpha level of .10. Table 7 shows the results of the analyses.

Table 7

Total Duration of Agonistic Behavior ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	F	η_P^2
Within subjects					
Period	5.76	2	2.88	3.19	.515
Environment	.825	1	.825	2.03	.403
Period X Environment	.101	2	.051	.084	.027
"error" w1 (Period)	5.43	6	.905		
"error" w2 (Environment)	1.22	3	.407		
"error" w3 (Period X Environment)	3.62	6	.603		
Total	17.0	20			

Note. η_P^2 = Partial eta squared. **p* < .10, ***p* < .05

There was no difference in total duration of agonistic behaviors among time period 1 (M = 1.58 min., SD = 1.15), time period 2 (M = .825 min., SD = .421), and time period 3 (M = .396 min., SD = .613), $F(2,6) = 3.19$, $p > .10$. There was also no difference in total duration of agonistic behaviors between inside (M = 1.12 min., SD = .814) and outside (M = .749 min., SD = .352) environments, $F(1,3) = 2.03$, $p > .10$. Additionally, there was no interaction between period and environment, $F(2,6) = .084$, $p > .10$.

Total Duration of Anxious Behavior

A two-way factorial ANOVA (3X2) was conducted with total duration of anxious behavior as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research questions of interest. All null hypotheses were tested at an alpha level of .10. Table 8 shows the results of the analyses.

Table 8

Total Duration of Anxious Behavior ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	*F*	η_P^2
Within subjects					
Period	4,477	2	2,238	4.95*	.622
Environment	6,202	1	6,202	10.9**	.784
Period X Environment	2,868	2	1,434	3.71*	.553
"error" w1 (Period)	2,716	6	453		
"error" w2 (Environment)	1,708	3	569		
"error" w3 (Period X Environment)	2,321	6	387		
Total	20,292	20			

Note. η_P^2 = Partial eta squared. *$p < .10$, **$p < .05$

There was a difference in total duration of anxious behaviors among period 1 ($M = 38.1$ min., $SD = 21.3$), period 2 ($M = 20.0$ min., $SD = 19.0$), and period 3 ($M = 4.64$ min., $SD = 1.77$), $F(2,6) = 5.97$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .622$.There was also a difference in total duration of anxious behaviors between inside ($M = 4.80$ min., $SD = 1.96$) and outside ($M = 36.9$ min., $SD = 20.8$) environments, $F(1,3) = 10.89$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .784$. Furthermore, there was a significant interaction between the time periods and the environments, $F(2,6) = 3.71$, $p < .10$. This difference was considered medium as indicated by the effect size measure partial eta squared, $\eta_P^2 = .553$.

Bonferroni pairwise comparisons were conducted to locate individual differences in total duration of anxious behavior among the time periods. Table 9 shows the results of the analyses.

Table 9

Total Duration of Anxious Behavior: Period Bonferroni Pairwise Comparisons

Period	Mean	1: Before Full Contact 38.1	2: Early Full Contact 20.0	3: Later Full Contact 4.64
1: Before Full Contact	38.1		NS	NS
2: Early Full Contact	20.0			NS
3. Later Full Contact	4.64			

Note. NS = not significant. *$p < .10$, **$p < .05$

The statistical power was not sufficient enough to detect a difference in total duration of anxious behavior among time periods in pairwise comparisons, although the omnibus ANOVA was significant.

Two simple effects tests were conducted to explore the nature of the interaction effects between time period and environment on anxious behavior. Table 10 shows the results of the first simple effects test.

Table 10

Total Duration of Anxious Behavior: Period X Environment Simple Effects Test One: Differences Between Environments Within Time Periods

Period	*F*	Hypothesis df	Error df	Sig.
1: Before Full Contact	8.91	1.00	3.00	.058**
2: Early Full Contact	4.26	1.00	3.00	.131
3: Later Full Contact	4.61	1.00	3.00	.121

Note. *$p < .10$, **$p < .05$

There was a difference in duration of anxious behavior between In (M = 9.75 min., SD = 2.59) and Out (M = 66.4 min., SD = 40.3) environments during time period 1: Before Full Contact, F (1,3) = 8.91, $p < .10$. There was no difference, however, in duration of anxious behavior between environments during time period 2: Early Full Contact, F (1,3) = 4.26, $p > .10$. Furthermore, there was no difference in duration of anxious behavior between environments during time period 3: Later Full Contact, F (1,3) = 54.61, $p > .10$. Table 11 shows the results of the second simple effects test.

Table 11

Total Duration of Anxious Behavior: Period X Environment Simple Effects Test Two: Differences Among Time Periods Within Environments

Environment	*F*	Hypothesis df	Error df	Sig.
In	33.3	2.00	2.00	.029**
Out	3.65	2.00	2.00	.215

Note. *$p < .10$, **$p < .05$

There was a difference in duration of anxious behavior among time periods observed within the inside environment, $F(2,2) = 33.3$, $p < .10$. There was no difference, however, in duration of anxious behavior among time periods observed within the outside environment, $F(2,2) = 3.65$, $p > .10$.

Bonferroni pairwise comparisons were conducted to locate individual differences among time periods in the inside environment. Table 12 shows the results of the analyses.

Table 12

Total Duration of Anxious Behavior: Inside Environment Bonferroni Pairwise Comparisons

Env.	Period		1: Before Full Contact	2: Early Full Contact	3: Later Full Contact
In		Mean	9.75	1.82	2.87
	1: Before Full Contact	9.75		**	*
	2: Early Full Contact	1.82			NS
	3. Later Full Contact	2.87			

Note. NS = not significant. *$p < .10$, **$p < .05$

There was a difference in duration of anxious behavior between period 1 in the inside environment (M = 9.75 min., SD = 2.58) and period 2 in the inside environment (M = 1.82 min., SD = 1.59), $p < .10$. There was also a difference in duration of anxious behavior between period 1 in the inside environment (M = 9.75 min., SD = 2.58) and period 3 in the inside environment

(M = 2.87 min, SD = 2.38), $p < .10$. There was no difference, however, in duration of anxious behavior between period 2 in the inside environment (M = 1.82 min., SD = 1.59) and period 3 in the inside environment (M = 2.87 min., SD = 2.38), $p > .10$ (See Figure 17).

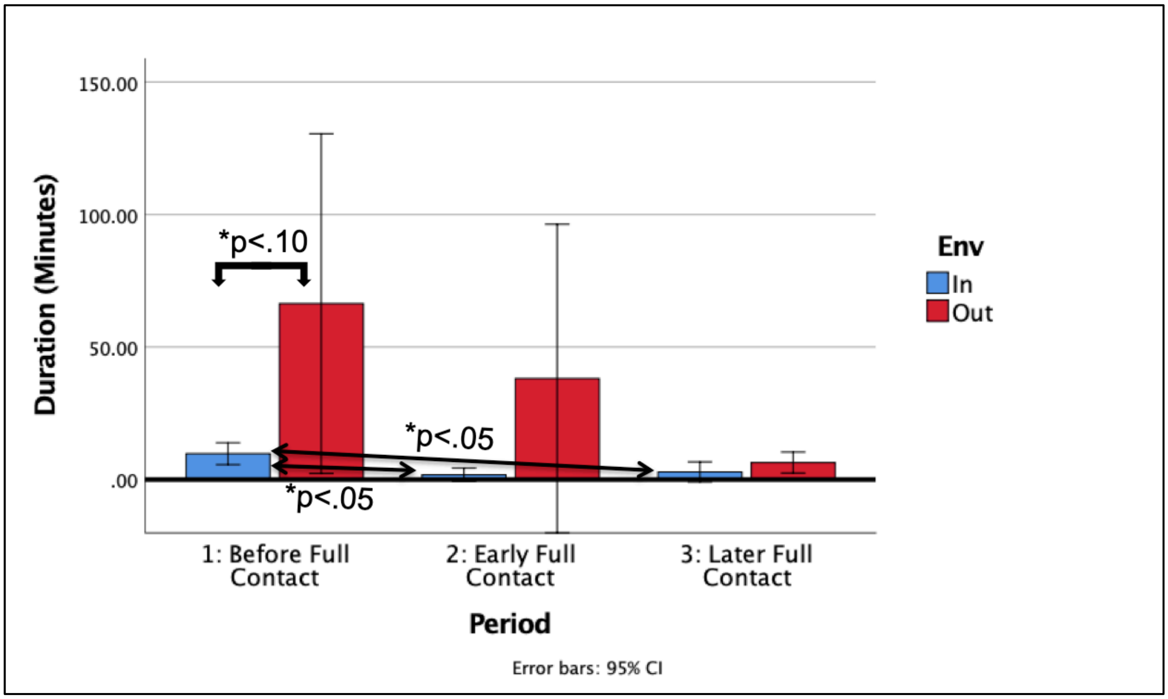

Figure 17. Anxious Behavior Graph. Interaction effect of time period and environment on total duration of anxious behavior. Standard errors are represented in the figure by the error bars attached to each column.

Total Duration of Undesirable Behavior

A two-way factorial ANOVA (3X2) was conducted with total duration of undesirable behavior as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research questions of interest. All null hypotheses were tested at an alpha level of .10. Table 13 shows the results of the analyses.

Table 13

Total Duration of Undesirable Behavior ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	*F*	η_P^2
Within subjects					
Period	26.4	2	13.2	1.79	.374
Environment	6.97	1	6.97	.287	.087
Period X Environment	20	2	9.99	2.85	.487
“error” w1 (Period)	44.1	6	7.36		
“error” w2 (Environment)	72.7	3	24.3		
“error” w3 (Period X Environment)	21.1	6	3.51		
Total	191.27	20			

Note. η_P^2 = Partial eta squared. **p* < .10, ***p* < .05

There was no difference in total duration of undesirable behaviors among time period 1 (*M* = 4.09 min., *SD* = 6.39), time period 2 (*M* = 2.04 min., *SD* = 3.13), and time period 3 (*M* = 1.73 min., *SD* = 3.08), $F(2,6) = 1.79$, $p > .10$. There was also no difference in total duration of undesirable behaviors between inside (*M* = 3.15 min., *SD* = 6.06) and outside (*M* = 2.08 min., *SD* = 2.57) environments, $F(1,3) = .29$, $p > .10$. Additionally, there was no interaction between period and environment, $F(2,6) = 2.85$, $p > .10$.

Total Duration of Locomotion

A two-way factorial ANOVA (3X2) was conducted with total duration of locomotion as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research questions of interest. All null hypotheses were tested at an alpha level of .10. Table 14 shows the results of the analyses.

Table 14

Total Duration of Locomotion ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	*F*	η_P^2
Within subjects					
Period	3,309	2	1,654	5.17*	.633
Environment	2,464	1	2,464	16.9**	.849
Period X Environment	1,669	2	835	16.2**	.844
"error" w1 (Period)	1,921	6	320		
"error" w2 (Environment)	438	3	146		
"error" w3 (Period X Environment)	309	6	51.5		
Total	10,110	20			

Note. η_P^2 = Partial eta squared. **p* < .10, ***p* < .05

There was a difference in total duration of locomotion among time period 1 (*M* = 33.0 min., *SD* = 23.6), time period 2 (*M* = 43.3 min., *SD* = 6.93), and time period 3 (*M* = 14.9 min., *SD* = 2.03), $F(2,6) = 5.17$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .633$. There was also a difference in total duration locomotion between inside (*M* = 20.3 min., *SD* = 7.35) and outside (*M* = 40.6 min., *SD* = 13.7) environments, $F(1,3) = 16.9$, $p < .10$. This difference was considered very large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .849$. Lastly, there was a significant interaction between the time periods and the environments, F(2,6) = 16.2, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .844$.

Bonferroni pairwise comparisons were conducted to locate individual differences in total duration of locomotion among the time periods. Table 15 shows the results of the analyses.

Table 15

Total Duration of Locomotion: Period Bonferroni Pairwise Comparisons

Period	Mean	1: Before Full Contact 33.0	2: Early Full Contact 43.3	3: Later Full Contact 14.9
1: Before Full Contact	33.0		NS	NS
2: Early Full Contact	43.3			**
3. Later Full Contact	14.9			

Note. NS = not significant. **p* < .10, ***p* < .05

There was a difference in total duration of locomotion between period 2 (*M* = 43.3 min., *SD* = 6.93) and period 3 (*M* = 14.9 min., *SD* = 2.03), $p < .10$. There was no difference, however, in total duration of locomotion between period 1 (*M* = 33.0 min., *SD* = 23.6) and period 2 (*M* = 43.3 min., *SD* = 6.93), $p > .10$. In addition, there was no difference in total duration of locomotion between period 1 (*M* = 33.0 min., *SD* = 23.6) and period 3 (*M* = 14.9 min., *SD* = 2.03), $p > .10$.

Two simple effects tests were conducted to explore the nature of the interaction effects between time period and environment on locomotion. Table 16 shows the results of the first simple effects test.

Table 16

Total Duration of Locomotion: Period X Environment Simple Effects Test One: Differences Between Environments Within Time Periods

Period	*F*	Hypothesis df	Error df	Sig.
1: Before Full Contact	2.22	1.00	3.00	.233
2: Early Full Contact	38.7	1.00	3.00	.008**
3: Later Full Contact	2.15	1.00	3.00	.239

Note. **p* < .10, ***p* < .05

There was no difference in duration of locomotion between environments during time period 1: Before Full Contact, $F(1,3) = 2.22$, $p > .10$. There was, however, a difference in duration of locomotion between In (*M* = 21.5 min., *SD* = 6.67) and Out (*M* = 65.1 min., *SD* =

12.2) environments during time period 2: Early Full Contact, F (1,3) = 38.7, $p < .10$. There was no difference in duration of locomotion between environments during time period 3: Later Full Contact, F (1,3) = 2.15, $p > .10$. Table 17 shows the results of the second simple effects test.

Table 17

Total Duration of Locomotion Behavior: Period X Environment Simple Effects Test Two: Differences Among Time Periods Within Environments

Environment	*F*	Hypothesis df	Error df	Sig.
In	7.59	2.00	2.00	.116
Out	44.9	2.00	2.00	.022**

Note. NS = not significant. **p* < .10, ***p* < .05

There was no difference in total duration of locomotion behavior among time periods within the inside environment, F (2,2) = 7.59, $p > .10$. There was, however, a difference in total duration of locomotion behavior among time periods within the outside environment, F (2,2) = 44.9, $p < .10$.

Bonferroni pairwise comparisons were conducted to locate individual differences among time periods in the outside environment. Table 18 shows the results of the analyses.

Table 18

Total Duration of Locomotion: Outside Environment Bonferroni Pairwise Comparisons

Env.	Period		1: Before Full Contact	2: Early Full Contact	3: Later Full Contact
		Mean	38.8	65.1	17.7
Out	1: Before Full Contact	38.8		NS	NS
	2: Early Full Contact	65.1			**
	3. Later Full Contact	17.7			

Note. NS = not significant. **p* < .10, ***p* < .05

There was a difference in total duration of locomotion between period 2 in the outside environment (M = 65.1 min., SD = 12.2) and period 3 in the outside environment (M = 17.7 min., SD = 5.07), $p < .10$. However, there was no difference in total duration of locomotion between period 1 in the outside environment (*M* = 38.8 min., *SD* = 31.2) and period 2 in the outside environment (*M* = 65.1 min., *SD* =12.2), $p > .10$. In addition, there was no difference in total duration of locomotion between period 1 in the outside environment (*M* = 38.8 min., *SD* =31.2) and period 3 in the outside environment (*M* = 17.7 min., *SD* = 5.07), $p > .10$ (See Figure 18).

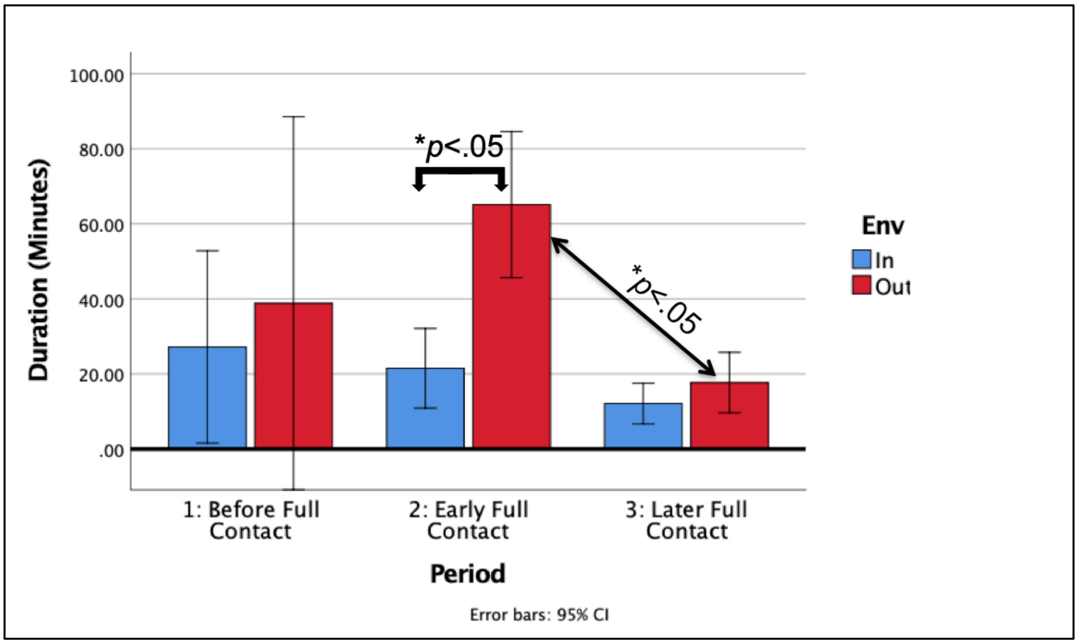

Figure 18. Locomotion Graph. Interaction effect of time period and environment on total duration of locomotion. Standard errors are represented in the figure by the error bars attached to each column.

Total Duration of Manipulation

A two-way factorial ANOVA (3X2) was conducted with total duration of manipulation as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research questions of interest. All null hypotheses were tested at an alpha level of .10. Table 19 shows the results of the analyses.

Table 19

Total Duration of Manipulation ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	*F*	η_P^2
Within subjects					
Period	2,415	2	1,207	4.72*	.611
Environment	.076	1	.076	.001	.000
Period X Environment	492	2	246	1.24	.292
"error" w1 (Period)	1,536	6	256		
"error" w2 (Environment)	287	3	95.7		
"error" w3 (Period X Environment)	1,189	6	396		
Total	5,919	20			

Note. η_P^2 = Partial eta squared. *$p < .10$, **$p < .05$

There was a difference in total duration of manipulation among time period 1 (*M* = 41.2 min., *SD* = 23.8), time period 2 (*M* = 26.9 min., *SD* = 6.95), and time period 3 (*M* = 16.7 min., *SD* = 6.48), $F(2,6) = 4.72$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .611$. There was no difference, however, in total duration of manipulation between inside (*M* = 28.2 min., *SD* = 9.51) and outside (*M* = 28.3 min., *SD* = 14.4) environments, $F(1,3) = 0.001$, $p > .10$. Furthermore, there was no interaction between period and environment, F (2,6) = 1.24, $p > .10$.

Bonferroni pairwise comparisons were conducted to locate individual differences in total duration of manipulation behavior among the time periods. Table 20 shows the results of the analyses.

Table 20

Total Duration of Manipulation: Period Bonferroni Pairwise Comparisons

Period	Mean	1: Before Full Contact 41.2	2: Early Full Contact 26.9	3: Later Full Contact 16.7
1: Before Full Contact	41.2		NS	NS
2: Early Full Contact	26.9			**
3. Later Full Contact	16.7			

Note. NS = not significant. *$p < .10$, **$p < .05$

There was a difference in total duration of manipulation between period 2 ($M = 26.9$ min., $SD = 6.95$) and period 3 ($M = 16.7$ min., $SD = 6.48$), $p < .10$. There was no difference, however, in total duration of manipulation between period 1 ($M = 41.2$ min., $SD = 23.8$) and period 2 ($M = 26.9$ min., $SD = 6.95$), $p > .10$. In addition, there was no difference in total duration of manipulation between period 1 ($M = 41.2$ min., $SD = 23.8$) and period 3 ($M = 16.7$ min., $SD = 6.48$), $p > .10$ (See Figure 19).

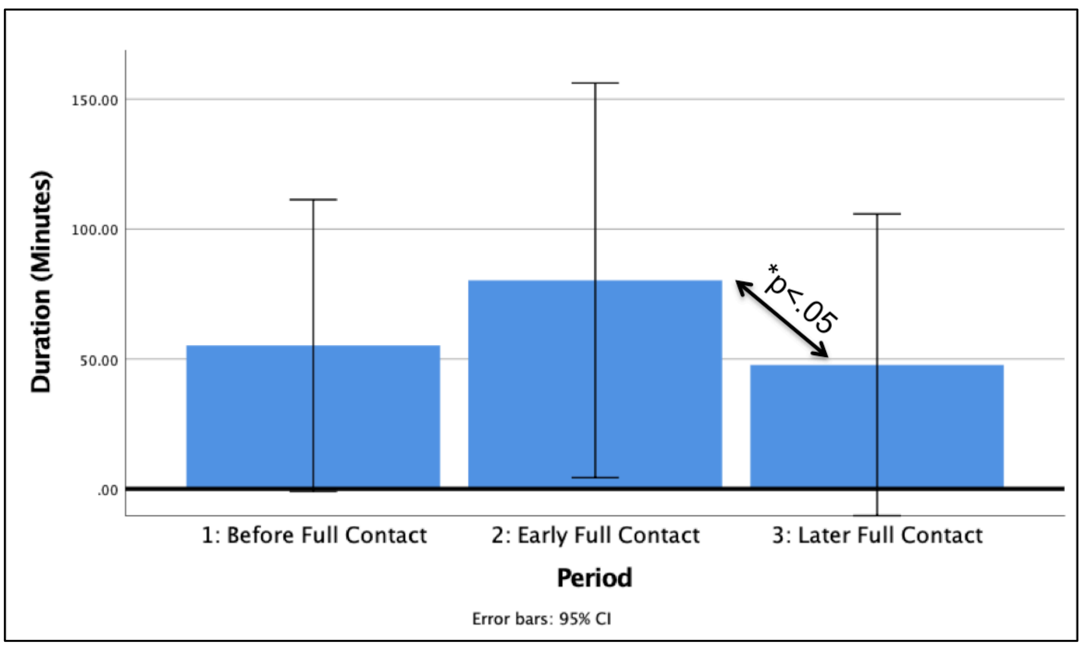

Figure 19. Manipulation Graph. Main effect of time period on total duration of manipulation. Standard errors are represented in the figure by the error bars attached to each column.

Total Duration of Stationary Behavior

A two-way factorial ANOVA (3X2) was conducted with total duration of stationary behavior as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research questions of interest. All null hypotheses were tested at an alpha level of .10. Table 21 shows the results of the analyses.

Table 21

Total Duration of Stationary Behavior ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	F	η_P^2
Within subjects					
Period	99,237	2	49,618	11.2**	.788
Environment	61,486	1	61,486	24.2**	.890
Period X Environment	142,804	2	71,402	24.5**	.891
"error" (Period)	26,687	6	4,448		
"error" (Environment)	7,629	3	2,543		
"error" (Period X Environment)	17,503	6	2,917		
Total	355,346	20			

Note. η_P^2 = Partial eta squared. *$p < .10$, **$p < .05$

There was a difference in total duration of stationary behaviors among period 1 (M = 174 min., SD = 61.4), period 2 (M = 280 min., SD = 43.7), and period 3 (M = 126 min., SD = 30.9), $F(2,6) = 11.2$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .788$. There was also a difference in total duration of stationary behaviors between inside (M = 143 min., SD = 29.9) and outside (M = 244 min., SD = 37.5) environments, $F(1,3) = 24.2$, $p < .10$. This difference was considered very large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .890$. Furthermore, there was a significant interaction between the time periods and the environments, $F(2,6) = 24.5$, $p < .10$. This difference was considered large as indicated by the effect size measure partial eta squared, $\eta_P^2 = .891$.

Bonferroni pairwise comparisons were conducted to locate individual differences in total duration of stationary behavior among the time periods. Table 22 shows the results of the analyses.

Table 22

Total Duration of Stationary Behavior: Period Bonferroni Pairwise Comparisons

Period	Mean	1: Before Full Contact 174	2: Early Full Contact 280	3: Later Full Contact 126
1: Before Full Contact	174		NS	NS
2: Early Full Contact	280			**
3. Later Full Contact	126			

Note. NS = not significant. *$p < .10$, **$p < .05$

There was a difference in total duration of stationary behavior between period 2 ($M = 280$ min., $SD = 43.7$) and period 3 ($M = 126$ min., $SD = 30.8$), $p < .10$. There was no difference, however, in total duration of stationary behavior between period 1 ($M = 174$ min., $SD = 61.4$) and period 2 ($M = 280$ min., $SD = 43.7$), $p > .10$. In addition, there was no difference in total duration of stationary behavior between period 1 ($M = 174$ min., $SD = 61.4$) and period 3 ($M = 126$ min., $SD = 30.8$), $p > .10$.

Two simple effects tests were conducted to explore the nature of the interaction effects between time period and environment on stationary behavior. Table 23 shows the results of the first simple effects test.

Table 23

Total Duration of Stationary Behaviors: Period X Environment Simple Effects Test One: Differences Between Environments Within Time Periods

Period	*F*	Hypothesis df	Error df	Sig.
1: Before Full Contact	.002	1.00	3.00	.971
2: Early Full Contact	122	1.00	3.00	.002**
3: Later Full Contact	.818	1.00	3.00	.432

Note. $^{*}p < .10$, $^{**}p < .05$

There was no difference in duration of stationary behavior between environments during time period 1: Before Full Contact, $F\,(1,3) = .002$, $p > .10$. There was a difference in duration of stationary behavior, however, between In ($M = 121$ min., $SD = 22.6$) and Out ($M = 440$ min., $SD = 70.5$) environments during time period 2: Early Full Contact, $F\,(1,3) = 122$, $p < .10$. There was no difference in duration of stationary behavior between environments during time period 3: Later Full Contact, $F\,(1,3) = .818$, $p > .10$. Table 24 shows the results of the second simple effects test.

Table 24

Total Duration of Stationary Behavior: Period X Environment Simple Effects Test Two: Differences Among Time Periods Within Environments

Environment	*F*	Hypothesis df	Error df	Sig.
In	15.1	2.00	2.00	.062*
Out	76.9	2.00	2.00	.013**

Note. NS = not significant. $^{*}p < .10$, $^{**}p < .05$

There was a difference in total duration of stationary behavior among time periods within the inside environment, $F(2,2) = 15.1$, $p < .10$. Additionally, there was a difference in total duration of stationary behavior within the outside environment, $F(2,2) = 76.9$, $p < .10$.

Bonferroni pairwise comparisons were conducted to locate individual differences in total duration of stationary behavior among the time periods. Table 25 shows the results of the analyses for the inside environment.

Table 25

Total Duration of Stationary Behavior: Inside Bonferroni Pairwise Comparisons

Env.	Period	Mean	1: Before Full Contact 173	2: Early Full Contact 121	3: Later Full Contact 135
In	1: Before Full Contact	173		**	NS
	2: Early Full Contact	121			NS
	3. Later Full Contact	135			

Note. NS = not significant. *$p < .10$, **$p < .05$

There was a difference in duration of stationary behavior between period 1 in the inside environment (M = 173 min., SD = 29.8) and period 2 in the inside environment (M = 121 min., SD = 22.6), $p < .10$. There was no difference, however, in duration of stationary behavior between period 1 in the inside environment (M = 173 min., SD = 29.8) and period 3 in the inside environment (M = 135 min, SD = 48.9), $p < .10$. Furthermore, there was no difference in duration of stationary behavior between period 2 in the inside environment (M = 121 min., SD = 22.6) and period 3 in the inside environment (M = 135 min, SD = 48.9), $p < .10$.

Bonferroni pairwise comparisons were conducted to locate individual differences in total duration of stationary behavior among the time periods. Table 26 shows the results of the analyses for the outside environment.

Table 26

Total Duration of Stationary Behavior: Outside Bonferroni Pairwise Comparisons

Env.	Period	Mean	1: Before Full Contact 175	2: Early Full Contact 440	3: Later Full Contact 118
Out	1: Before Full Contact	175		NS	NS
	2: Early Full Contact	440			**
	3. Later Full Contact	118			

Note. NS = not significant. *$p < .10$, **$p < .05$

There was a difference in duration of stationary behavior between period 2 in the outside environment (M = 440 min., SD = 70.5) and period 3 in the outside environment (M = 118 min., *SD* = 16.0), $p < .10$. There was no difference, however, in duration of stationary behavior between period 1 in the outside environment (*M* = 175 min., *SD* = 112) and period 2 in the outside environment (*M* = 440 min., *SD* = 70.5), $p < .10$. Furthermore, there was no difference in duration of stationary behavior between period 1 in the outside environment (*M* = 175 min., *SD* = 112) and period 3 in the outside environment (*M* = 118 min., *SD* = 16.0), $p < .10$ (See Figure 20).

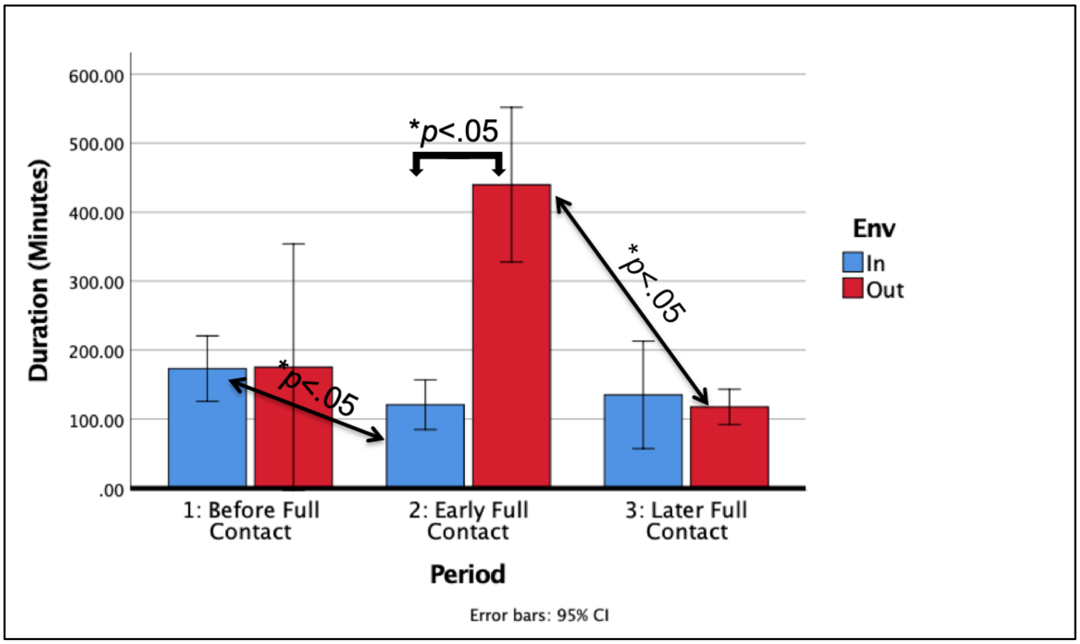

Figure 20. Stationary Behavior Graph. Interaction effect of time period and environment on total duration of stationary behavior. Standard errors are represented in the figure by the error bars attached to each column.

Total Duration of Other Behavior

A two-way factorial ANOVA (3X2) was conducted with total duration of other behavior as the dependent variable. Time period and environment were used as independent variables. Both independent variables were repeated measures. Thus, every subject was observed multiple times across factor levels. The time period factor had three levels (period 1: before full contact, period 2: early full contact, and period 3: later full contact). The environment factor had two levels (inside and outside). Thus, a two-way factorial ANOVA (3X2) was the most appropriate statistical method of analysis to answer the research questions of interest. All null hypotheses were tested at an alpha level of .10. Table 27 shows the results of the analyses.

Table 27

Total Duration of Other Behavior ANOVA Summary Among Periods and Between Environments

Source of Variation	SS	df	MS	*F*	η_P^2
Within subjects					
Period	3.22	2	1.61	1.97	.396
Environment	1.21	1	1.21	4.77	.614
Period X Environment	.347	2	.174	.053	.017
"error" (Period)	4.91	6	.818		
"error" (Environment)	.760	3	.253		
"error" (Period X Environment)	19.6	6	3.27		
Total	30.0	20			

Note. η_P^2 = Partial eta squared. **p* < .10, ***p* < .05

There was no difference in total duration of other behaviors among time period 1 (*M* = .177, *SD* = .216), time period 2 (*M* = .960, *SD* = 1.04), and time period 3 (*M* = .948, *SD* = .700), $F(2,6) = 1.97$, $p > .10$. There was also no difference in total duration of undesirable behaviors between inside (*M* = .919, *SD* = .628) and outside (*M* = .471, *SD* = .469) environments, $F(1,3) = 4.77$, $p > .10$. Additionally, there was no interaction between period and environment, $F(2,6) = .053$, $p > .10$.

Discussion

The lifespan of gorillas in human care can range from 40 to 50 years of age. Therefore, the death of a silverback has been a rare occurrence in zoos. Only a handful of zoos have studied the phenomena and even then only a few of those have also been able to study the effects of introducing a new male to the remaining group. Based on previous literature, it was predicted that when Mbundi was re-introduced to the group, agonism would increase initially and then decrease over time. In addition, as time passed, it was predicted that there would be an increase of affiliative behaviors and a decrease of anxious behaviors.

Although, as other researchers have previously found (Margulis *et al.*, 2002; Johnstone-Scott, 1998), time spent in affiliative behaviors did increase, but only between Period 1 and 2, and then only outdoors. This increase may have occurred between the pre-introduction and early introduction due to the stressfulness of introducing a new member to the family group. In addition, the increase in affiliative behavior was only observed in the outside environment. The GPZ gorilla exhibit has much more space available outside than the inside enclosure. The inside enclosure is also considered the gorillas "bedroom" due to the amount of time spent there resting. Affiliative behavior may have occurred more in the outside environment due to the gorillas being much more active and engaged in behaviors outdoors than compared to the inside environment.

In the wild female gorillas are usually not related to one other due to females emigrating to other groups (Harcourt *et al*., 1976; Stewart & Harcourt, 1987). As a consequence, affiliative behavior between most females is quite rare. However, female gorillas in human care are not able to emigrate on their own and are therefore more likely to be related to the other females in their group. Harcourt (1979) observed two related females were friendlier with one another than were the other females among themselves. In fact, primates tend to engage in more affiliative behavior during taxing situations to help cope with stress (de Waal, 1984). The female gorillas in GPZ are closely related to one another and the increased affiliative behavior may suggest that this occurred to help reduce the social tension that was created by re-introducing Mbundi to the group.

In addition to coping with stress, another factor that may have caused affiliative behaviors to increase was use of birth control with the females. Birth control is commonly used to control reproduction in animals housed in zoo institutions (Glatson, 1998; Porton, Asa, & Baker, 1990; Porton & DeMatteo, 2005). When female gorillas are on birth control, estrous behaviors are suppressed. Thus, when females are taken off contraceptives, they are more likely to engage in estrous behaviors with males (Sarfaty, Margulis, & Atsalis, 2012). The GPZ females were released from contraceptives on July 18, 2018. Consequently, the increase in affiliative behavior after Mbundi was introduced may suggest that the females engaged in estrous behavior, which increased time spent being near the silverback (See Figure 21).

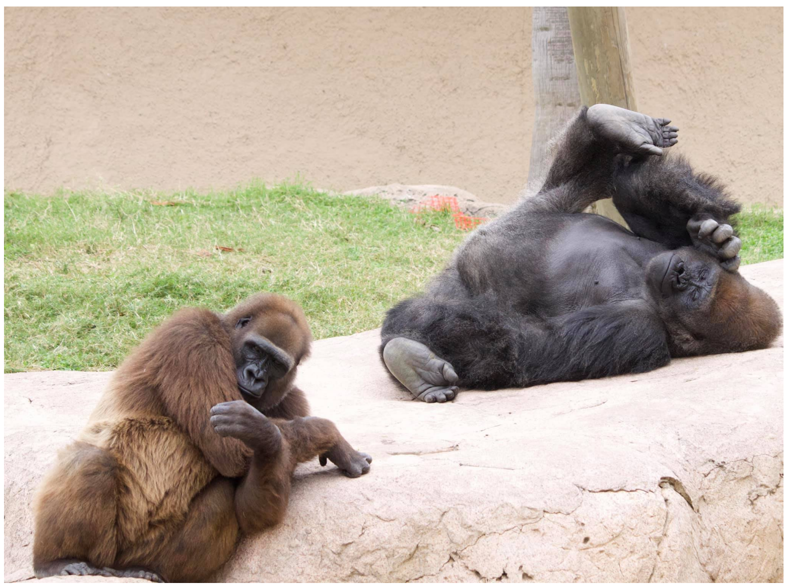

Figure 21. Mbundi and Margaret. Margaret sitting near Mbundi. Photo taken by Ruben Hernandez.

Surprisingly, in contrast to most reports (Hoff *et al*., 1996; Johnstone-Scott, 1998; Margulis *et al*., 2002) levels of agonism were low in all conditions in this study. Similarly, Weerd *et al*., (2010) found no increase in agonism after the new silverback at Artis Royal Zoo was introduced to two females. There is a possibility that this study did not detect an increase in agonism due to the way behaviors were measured (as total amount of time subjects spent engaging in behaviors). Agonistic behaviors can occur rapidly and end quickly. Thus, when duration of behaviors is used it may underestimate the occurrence of agonism since the behavior could have occurred, but the duration was not long enough to be found significant.

In the current study, anxious behaviors were defined as the focal subject performing any of the following: AutoGroom, hair pull, hair pull-AutoGroom, scratch and/or submit/greet. Undesirable behaviors were defined as the focal subject performing coprophagy and/or regurgitation/reingestion. Animals can also engage in undesirable behaviors when coping with stress, however, these behaviors were separated into their own category due to how maladaptive they could become. Manipulation was defined as the individual closely investigating some physical object/s (may have included body parts), handling it/them in some way. These types of behaviors are usually categorized under solitary behaviors in literature (Hoff *et al*., 1996, 1998; Less *et al*., 2010; Weerd *et al.*, 2010).

Consistent with previous findings (Margulis *et al.*, 2002; Johnstone-Scott, 1998; Weerd *et al.*, 2010), time spent in anxious behaviors did decrease, but only between Period 1 and 2 and Period 1 and 3, and then only indoors. The decrease in anxious behaviors between Period 1 when compared to both Period 2 and 3 demonstrates that Mbundi brought stability back to the group after he was re-introduced. For example, Weerd *et al.* (2010) observed a decrease in negative social behavior and stereotypic behavior for both female gorillas after the introduction of the new male. Furthermore, the decrease in anxious behavior in the present study was found only in the indoor environment. This may have occurred due limited space in the indoor enclosure. When the gorillas are indoors, they are closer to one another than compared to when they are outdoors. Therefore, after Mbundi was introduced there was less tension observed in the group and over time the gorillas could engage in other behaviors (e.g., affiliative behaviors) since they were no longer anxious.

Unexpectedly, in contrast to most studies (Hoff *et al*., 1996, 1998; Weerd *et al.*, 2010; but see Less *et al*., 2010), time spent in manipulation did decrease, but only between Period 2 and 3. There was no difference, however, in total duration of manipulation between inside and outside environments. It is possible that the observed decrease in manipulation between Period 2 and 3 may be caused from the overall increase of affiliative behavior, which provided greater social interaction opportunities. Thus, the decrease in anxious behaviors and manipulation, found after Mbundi was re-introduced, might suggest that gorillas were now less anxious around one another and that the new silverback had established control and restored stability to the group.

Finally, there was no significant change in undesirable behaviors, which was consistent with previous findings (Hoff *et al*., 1996, 1998; but see Less *et al*., 2010). When animals in human care engage in undesirable behaviors these are often considered signs of environmental deficiencies (Leeds, Elsner, & Lukas, 2016). The low levels of undesirable behavior may suggest that the females housed at GPZ did not frequently engage in those types of behaviors due to their environments being properly enriched. Self-directed behaviors, as those listed in the anxious category, are indicative of tension in primates (Maestripieri, Schino, Aureli, & Troisi, 1992). It may be possible that the females may not have needed to engage in undesirable behaviors to help cope with stress, but instead other behaviors were used (e.g., auto grooming, hair pulling, scratching).

Although, as other researchers have previously found (Hoff *et al*., 1996; Weerd *et al.*, 2010), time spent in locomotion did decrease, but only between Period 2 and 3, and then only outdoors. The decrease in locomotion may have occurred between Period 2 and 3 due to the gorillas becoming more familiar with one another as time passed which may have caused their anxiety to decrease and they therefore did not need to move around so much. This decrease in locomotion was observed only in the outdoor environment. This decrease may have been greater than that in the indoor environment because the gorillas have more space to move around in than the indoor environment. In addition, consistent with previous findings (Hoff *et al*., 1996; Weerd *et al.*, 2010), time spent in stationary behaviors did decrease as well, but only between Period 1 and 2 in the indoor environment and between Period 2 and 3 in the outdoor environment. The decrease in stationary behaviors may have occurred between Period 1 and 2 in the indoor environment due to the limited space and the gorillas increased anxiety revolving around Mbundi's introduction which occurred in Period 2. The decrease in stationary behaviors between Period 2 and 3 may have also occurred in the outdoor environment due to the gorillas becoming more familiar with one another and having more space available to engage in other behaviors.

Stationary behaviors were defined as the focal subject being passive and not performing any of the other scoreable behaviors in the ethogram. The decrease in stationary behaviors suggests that the GPZ gorillas spent more time in other scoreable behaviors (e.g., affiliative behavior). Individuals react and adapt differently to stress by using certain coping strategies such as proactive or reactive coping (Ferreira *et al*., 2016). High levels of locomotion and rapid attack behaviors characterize proactive animals, while low levels of aggression and decreased activity characterize reactive animals (Koolhaas *et al*., 2010). The GPZ gorillas had low levels of locomotion and stationary behaviors in the later full contact period, which may suggest that the re-introduction of Mbundi became less stressful over time and coping strategies were not needed anymore. Other behaviors (e.g., copulation and unusually aggressive behaviors) were also examined, however there was no significant change observed. These behaviors may have not been found to be significant due to way the behaviors were measured which may have underestimated their occurrence.

Overall, the second attempt to introduce Mbundi to the three adult females was shown to be a successful. The increases in affiliative behaviors, decreases in anxious behaviors, and overall low levels of agonism suggest that Mbundi has assumed control and restored stability to the group. Mbundi has been allowed full access to his family group since May 2018 and has sired two offspring with two of the females in his group (See Figure 22).

Figure 22. Mbundi's Offspring. Martha and Margaret with their infants. Photo taken by the Gladys Porter Zoo.

CHAPTER V

GENERAL DISCUSSION AND CONCLUSIONS

The following chapter will compare the results from the current study with the results of the first introduction attempt. It is important to note that a detailed behavioral analysis such as the one conducted in this study was not conducted on data from the first introduction. Sections include General Discussion, Conclusion, and Suggestions for Future Research.

General Discussion

There are many factors that differ between the first introduction attempt and the second, successful one: Mbundi's familiarity with females, Mbundi's age, number of silverbacks in the facility, group size, female status hierarchy, and the presence of a juvenile male unrelated to Mbundi. I will discuss each factor in detail and examine how each of these differences made the second introduction attempt successful.

Mbundi's Familiarity with Females

I would like to begin with Mbundi's history and the experience he had socializing with female gorillas (Kansas City Zoo, 2014). Mbundi was initially housed in a family group at the Calgary Zoo. This group was made up of a silverback (his sire), three adult females (one of which was his dam), an unrelated black back, two half siblings, and one full sibling. In 1999, at the age of six, Mbundi was transferred, along with his half-brother N'tondo, to the Kansas City Zoo and they were placed in a bachelor group with an older male named Radi. However, once the brothers reached adolescence they became too aggressive with Radi and were separated from him in 2005. The brothers then became a dyad group. From 2005 to 2010, the facility the brothers were housed in only contained male gorillas.

In the fall of 2010, the Kansas City Zoo received two females to pair with Radi and in 2012, a third female was added to his group. A small increase in Mbundi's display behaviors was observed when the females were initially introduced into the facility. These behaviors were mostly directed towards the females (Kansas City Zoo, 2014b). In 2014 Mbundi was transferred to the Gladys Porter Zoo.

Although Mbundi had grown up in a family group with females, he had never been housed with females as an adult. As an adult he was housed in the same facility as females, but these females were placed in different group. Therefore, the intense aggressive encounters that occurred after Mbundi was first introduced to the GPZ family group may suggest that his lack of socialization with females as an adult caused him to react more intensely than he should have. Not being familiar with females, he had not learned how to react appropriately towards them. Male gorillas are much larger than female gorillas and are almost twice their weight (Rowe, 1996). These extreme physical differences make male gorillas almost twice as strong as female gorillas and potentially dangerous to them.

When the first introduction failed, a decision was made to retreat to earlier stages of the socialization process, allowing protected contact only between Mbundi and his intended group. The prolonged period of protected contact allowed Mbundi and the group members to become better familiarized with one another in a safe environment. The increased familiarity between Mbundi and the group may have helped make the second introduction attempt a success. During the first introduction agonistic behaviors did not decrease and Mbundi was removed from the group. However, the significant decrease in agonistic behavior in the second attempt suggests that Mbundi was learning to control his strength and was eventually able to bring stability to the group.

Mbundi's Age

Mbundi was 21-years-old when the first introduction took place. By the time the second introduction was initiated, three years had passed and Mbundi was now 25-years-old. When comparing both introduction attempts the success of the latter one may suggest that Mbundi's increase in age, and presumably maturity, helped make the second attempt smoother. When the first introduction took place Mbundi may have not been mature enough fully understand what his role was in the group. But during the three years between the first and second introduction Mbundi matured and was able to learn what his role required him to do. He was then able to take control of the group.

Number of Silverbacks in the Facility

In the wild, both male and female gorillas emigrate from their natal groups once they reach maturity (Harcourt et al., 1976), although there have been cases of multiple related silverbacks (e.g., father and son) living in a same group (Falk, 2000). However, it is still considered "rare" for males to form bachelor groups in the wild and these groups are generally thought to disband once males reach maturity (Robbins, 1996). Furthermore, bachelor groups are thought to be nonexistent in western lowland gorillas and instead emigrating males become solitary (Parnell, 2002).

Gorillas in human care are not able to emigrate on their own and are therefore transferred to other zoos to form new groups. These institutions may have more than one group housed in their facility, which can include mixed-sex family groups and/or bachelor groups. When Mbundi first arrived at the GPZ, three other silverbacks were present in the gorilla facility but were separated from his intended family group. These three silverbacks were related to one another. The addition of Mbundi, who was new and unrelated to the group, increased the level of agonistic behaviors (in the form of displays) among all the silverbacks in the facility. The zookeepers attempted to mitigate the agonistic behavior by limiting visual contact between Mbundi and the other silverbacks by placing a curtain between them; however, they could still smell and hear each other. The increased agonism between the silverbacks and Mbundi may have consequently increased Mbundi's anxiety level. This then could have contributed to increased agonism between Mbundi and the family group during the first introduction attempt.

By the time the second introduction attempt took place, two of the three silverbacks had been transferred to other zoos. These silverbacks were much younger than the remaining silverback, Lamydoc, who was 55-years-old at the time. Lamydoc is the founder male of Mbundi's intended family group and when the second attempt was initiated his activity level was low due to his advanced age. The reduced number of silverbacks in the facility during the second introduction may have made Mbundi less anxious and aggressive than when compared to the first was introduction attempted.

Decrease in Group Size

Mbundi's first attempted introduction in 2015 was to a group of six gorillas, comprised of five adult females and one juvenile male. During the interim between the first and second introduction attempts, the size of Mbundi's intended group declined from six to three after two of the animals, one adult female and the juvenile male, were moved to a different group (and, ultimately, to different zoos) and the death of one of the adult females. The resulting, smaller group was, thus, comprised of only three adult females by 2018. The reduction in group size may have made it easier for Mbundi to manage and take control of the group.

Female Status Hierarchy

At the time of the first introduction, the family group included: Penney, age 29 years, Martha, age 26 years, Kiazi, age 17 years, Samantha, age 9 years, Margaret, age 8 years and T.J., age 3 years. Four of the five females were related to one another. Penney and Martha are full sisters. Penny and Samantha are mother and daughter as is Martha and Margaret. The former silverback, Moja, sired both Samantha and Margaret. Kiazi was transferred to the GPZ on October 19, 2011 on breeding loan from the Cincinnati Zoo and was the only female who was unrelated to the rest of the group. When Moja was alive, Martha was observed to be the groups dominant female and was always supported by Moja when quarrels with the other group members occurred. Kiazi, an unrelated female, was lower ranking. However, when Moja passed in 2013, Kiazi was able to disrupt the social hierarchy of the group.

With Moja gone, Martha no longer had the support of a silverback. Kiazi began to harass the dominant female and was supported by Samantha. This harassment continued even during Mbundi's introduction in 2015. The shifting female hierarchy in addition to the introduction of Mbundi may have caused the first introduction to be highly more stressful that it might have been had the female group been more stable at the time. In 2016, Kiazi passed away following an accident that resulted in a broken arm and subsequent complications. Based on the groups behavior during the first introduction the zoo staff decided to form a new group with T.J. and Samantha as its members, thus, the family group during the Mbundi's second introduction attempt consisted of: Penney, Martha and Margaret. With Kiazi gone, Martha became the dominant female once again. The stability among the related females during the second introduction may have facilitated the success of this attempt.

Presence of a Juvenile Male Unrelated to Mbundi

In the first introduction, Mbundi's new group included a juvenile who was sired by the former silverback Moja. The young juvenile, named T.J., was 3-years-old at the time. In the wild when a new male gorilla takes over a group of females, he may commit infanticide, which causes the females, who are breastfeeding, to return back into estrous, and allows the male to sire offspring of his own (Yamagiwa, Kahekwa, & Basabose, 2009).

During the first introduction intensely aggressive incidents occurred that consequently halted Mbundi's socialization process. One of these episodes was apparently directed towards T.J. who received a wound in his pelvic area. The keepers were not present when this incident occurred and therefore there was no proof that the attacker was Mbundi. However, before Mbundi was introduced this type of attack had not occurred among the group members. Mbundi's presumed victimization of T.J. during the first introduction may suggest that Mbundi may have attacked T.J. in order to bring Martha back into estrous to sire offspring of his own.

In 2016, T.J. was removed from the family group to form a new group with his half sibling Samantha. Then in 2018 Mbundi's socialization process was restarted and his group now was made up of three adult females: Penney, Martha and Margaret. The removal of T.J. from the group was intended to keep the juvenile safe and reduce the level of aggression that Mbundi might display towards the remaining group members. The presence of T.J. in the first introduction may have played a major role in why this attempt was a failure and why his removal in the second introduction made that attempt a success.

Conclusion

The earlier attempt at an introduction was halted primarily as a result of aggressive behavior that resulted in injuries deemed unacceptably severe. A number of factors differed between that attempt and the second, successful, one: Mbundi's familiarity with females, Mbundi's age, the number of silverbacks in the facility, group size, female hierarchy, and the presence of an unrelated juvenile (See Figure 23). From this study, we learned that the prolonged period of protected contact, reduced group size, Mbundi maturing and the decrease of other silverbacks in the facility might have facilitated group formation. However, I am not sure if the second introduction would have been successful even if some of the differences between these attempts had not been present, such as group size and the three silverbacks still being present in the facility.

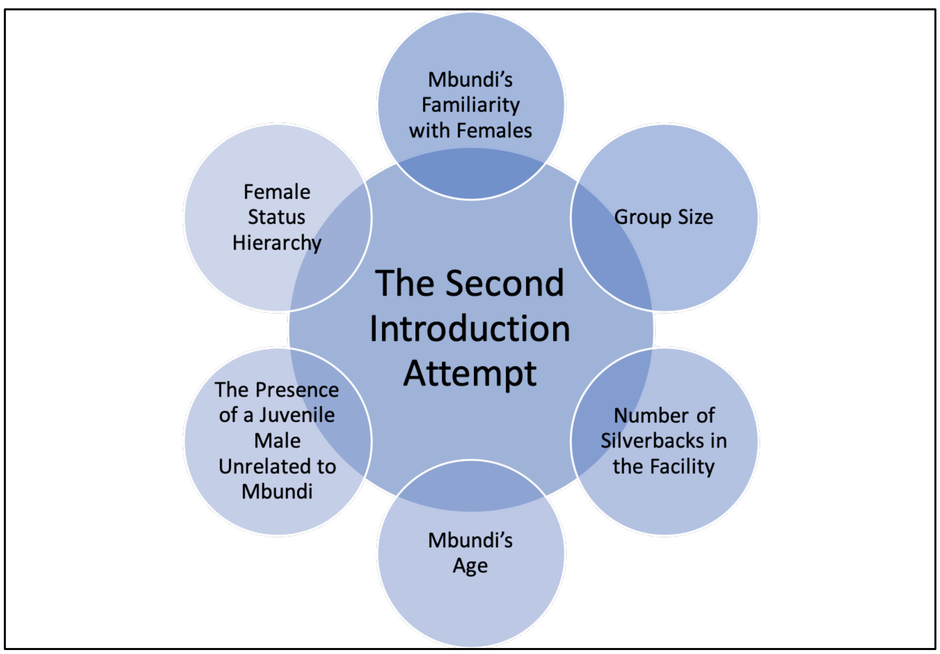

Figure 23. Factors Affecting the Second Introduction Attempt.

Although the first introduction had to be terminated, the second introduction attempt was highly successful. The increases in affiliative behaviors, decreases in anxious behaviors, and overall low levels of agonism suggest that Mbundi has assumed control and restored stability to the group (See Figure 24). Mbundi has now been allowed full access to his family group of three adult females since May 2018 and has sired two offspring from two of the three adult females in his group.

As silverbacks in human care become older, studies such as the current one may help provide a better understanding of the role a silverback plays within their family group. Finally, it may be concluded that understanding the behavioral responses of group members when group structures change can better prepare zookeepers to plan their management strategy when periods of social change are unavoidable.

Figure 24. Mbundi's Family Group. Mbundi sitting alongside the three adult females and their offspring. Photo taken by Ruben Hernandez.

Suggestions for Future Research

Undesirable & Anxious Behavior Category

This study placed coprophagy and regurgitation/reingestion behaviors in the undesirable behavior category. A reason these types of behaviors occur, however, may be due to the presence of stimuli that are viewed as stressful by the animal (Mason, 1991). Therefore, these behaviors could also have been placed in the anxious behavior category. There were no significant differences observed for the undesirable behavior category even though these behaviors did occur. It is suggested that future studies place undesirable behaviors and anxious behaviors into a single category or that category results be combined in order for these behaviors to be better represented in the results.

Measurement of Behaviors

Behaviors that occur rapidly, such as agonistic behaviors, are regarded as behavioral events and behaviors that have significant duration are considered behavioral states (Altmann, 1974). In the current study durations of bouts of behavior was used to measure each dependent variable. This type of measurement may have underestimated the occurrence of certain behaviors since they occurred too briefly to produce significant outcomes. In the future, I would like to go back to the raw data sheets and use frequency counts to measure such behaviors.

Detailed Behavioral Analysis of Frist Introduction

A detailed behavioral analysis was conducted on the data from Mbundi's second introduction attempt; however, one was not done on the data from the first introduction attempt. I would like to conduct a two-way factorial ANOVA (3X2) on the data from the first introduction attempt by using time period as the first factor and environment as the second factor.

Animal Personality

The observed results of this current study may have been biased by the personalities of the subjects. Animal personality is defined as animals displaying consistent individual differences in behavior over time and across environmental changes (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Therefore, the field of animal personality can help describe the variance in measures of animal behavior (Beekman and Jordan, 2017). In the future, I would like to conduct a separate detailed behavior analysis that focuses on the individual differences of each subject when Mbundi was re-introduced.

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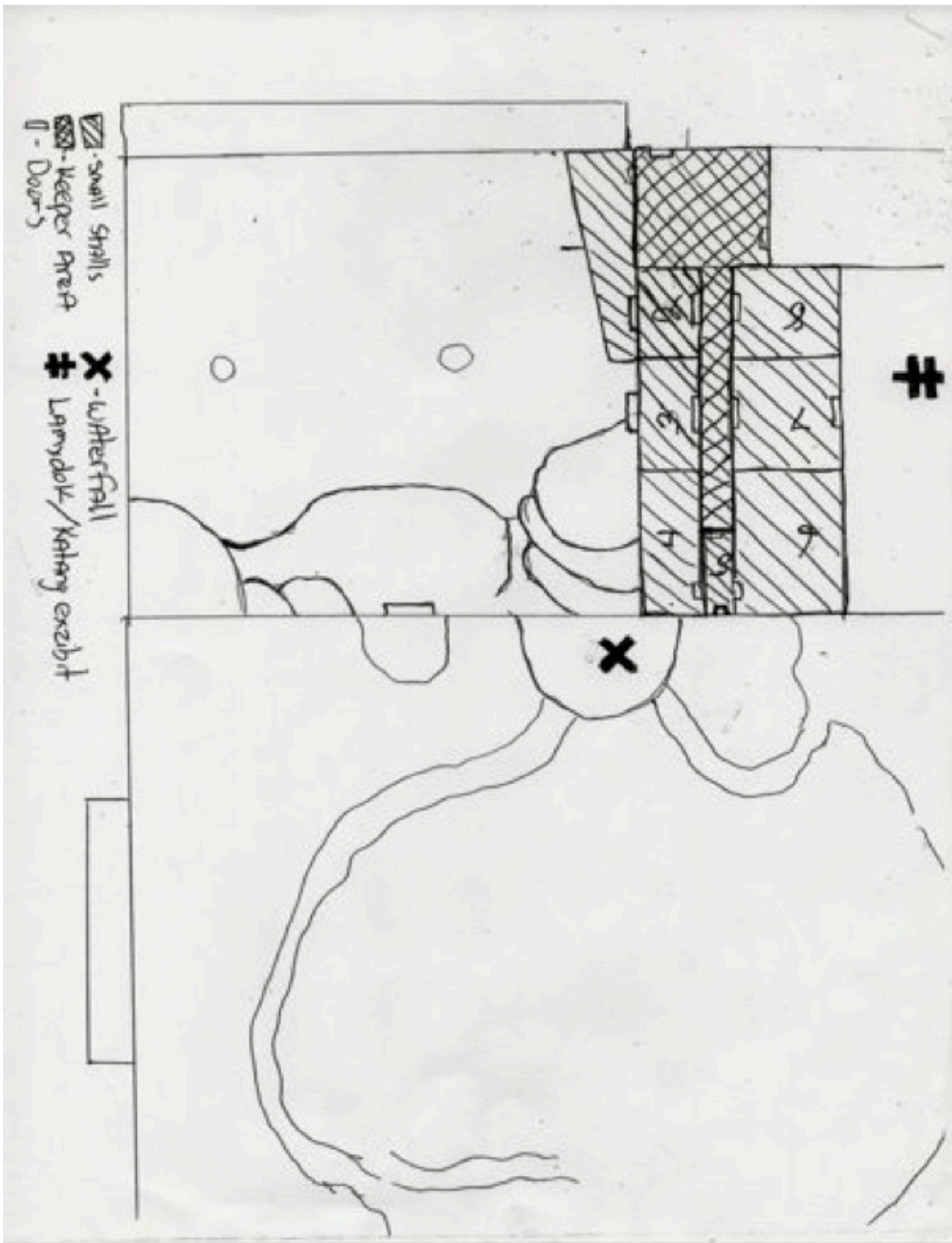
APPENDIX A

APPENDIX A

GORILLA EXHIBIT LAYOUT



APPENDIX B

APPENDIX B

MBUNDI ET AL., TIMELINE

Nov. 19, 2014	Arrives at Gladys Porter Zoo
Jan. 29, 2015	Moved to off-exhibit living space #8
Mar. 19, 2015	Shifted to off-exhibit living space #2
Apr. 14, 2015	Introduced to family group inside building
Apr. 23, 2015	Outdoors with group
May 3, 2015	Observed biting Kiazi
May 5, 2015	Observed by a student fighting with Penney
May 7, 2015	Out with group (without T.J.)
May 14, 2015	Bit Margaret a few days previously (wound intensity: 5)
Feb. 15, 2016	Lamydoc (starter silverback), Martha, T.J., Kiazi formed new group
Apr. 18, 2016	Lamydoc separated from new group
Apr. 30, 2016	Switched Margaret for Kiazi in new group
Jul. 26, 2016	Nzinga and Bangori (other silverbacks) transferred to new zoo
Aug. 14, 2016	Kiazi injured sometime during previous night (left arm)
Aug. 20, 2016	Kiazi died
Aug. 25, 2016	Martha, Margaret, & T.J. reintroduced to Penney & Samantha
Jan. 22, 2017	Switch doors btw off-exhibit living space #2 & # 3 left open for Mbundi
Apr. 12, 2018	Zookeeper meeting about reintroducing Mbundi
May 1, 2018	Day 1 of Mbundi reintroduction to Penney, Martha & Margaret

APPENDIX C

APPENDIX C

ETHOGRAM

Behavior	Definition
G	AlloGroom: one individual works through hair of another individual using fingers, teeth, and/or lips. Record receiver if possible.
AuG	**Au**to**G**room: individual self-grooms. Exclude occasional brief body scratching or nose swipes, but include light scratching or facial cleaning that is intensive or repeated frequently within a single bout.
B	**B**eg: individual solicits "contraband" from zoo visitor(s), by means of, e.g., hand extension or hand claps. Do not include begging from another animal in this category (see contact close or contact touch below).
CC	**C**ontact **C**lose: focal animal is near another animal (within "easy arm's reach," i.e., within approximately 1 meter from one another), but they are not actually touching one another. Include the close approach usually made when one animal begs something from another. Record other participant, if possible.
CT	**C**ontact **T**ouch: focal animal is touching or being touched by another animal. Include all types of holding, carrying, or huddling. Do not include grooming, contacts made in social play, or genital inspections in this category (see allogroom above; and social play and genitalinspect below). Record animal(s) contacted, if possible. Note instances of nursing in mother/infant pairs. If contact between mother and infant is broken, record who initiated the break
CTA	**C**ontact **T**ouch – **A**ggressive: focal animal touches or is touched by another animal in a manner that is rough or intense, e.g., slaps, swats. Action is typically brief and does not result in a prolonged encounter. Do not include agonistic contacts made in the context of full displays (see display or respond to display, below). If focal animal hits an inanimate object, record as hit/kick (see below). If agonistic behavior is prolonged or results in an actual fight, record as other and accompany the code with a narrative description. Record other participant, if possible.

Behavior	Definition
Cop	Coprophagy: eating one's own feces or drinking one's own urine, or consuming wastes that have been immediately captured from another. Record the consumption of old feces or urine as instances of forage (see below).
Dsp	**Disp**lace: one individual approaches another causing the second to move away from his/her present position, which is then occupied by the first. Record type of displacement, i.e., simple displace (**Dsp**), displacement accompanied by physical contact ranging from a light **T**ouch to a push or shove (**Dsp T**), displacement accompanied by **V**ocalization (**Dsp V**).
D	**D**isplay: a complex series of behaviors, typically performed by an adult male, which may include an upright stance, piloerection, swaggering, running (bipedally or quadrupedally), chest beating (in gorillas), ground slaps, door pounding, etc. Occasionally accompanied by loud vocalization which, under these conditions, is not recorded separately (see vocalize below).
Dr	**Dr**ink: individual has lips in contact with water in pool or is bent over water. Do not include drinking urine in this category (see coprophagy above).
F	**F**orage/eat: individual repeatedly picks through grass, gravel, or dirt with fingers or lips selecting items, placing them in the mouth, and, apparently, eating them. Record object foraged, if possible.
Gen	**Gen**ital inspect: individual investigates the genital region of another animal, visually, olfactorily, and/or manually, or is so inspected by another. This is a much more stylized behavior than is simple grooming of the genital region; genital inspections are usually much briefer than grooming sessions and the receiver is usually standing quadrupedally rather than lying or sitting down. Record other participant, if possible.
HP	**H**air **P**ull: one animal plucks individual hairs from the animal being "groomed", frequently with the teeth. The movements associated with hair pulling consist generally of short, sharp jerks of the head or hand in contrast with the more gentle movements associated with grooming. Record other participant, if possible.
HPA	**H**air **P**ull - **A**utogroom: a self-directed version of hair pulling (see above).

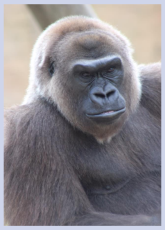
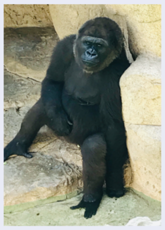
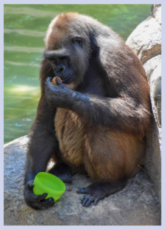
Behavior	Definition
I	**I**nteract: attention is directed to zoo visitor(s) that is different from begging (see above). May include approaches to calls, mild displays, playing games at the windows, etc. Do not include passive observations of visitors (or of you).
L	**L**ocomote: individual changes location by any active means by at least one body length; for example, walking, running, climbing, pirouetting, dangling by one arm, etc.
M	**M**anipulate: individual closely investigates some physical object/s (may include body parts, e.g., feet), handling it/them in some way. Object does not necessarily move (e.g., ladder on climbing structure). May include placing objects in the mouth, but animal is clearly "playing with" rather than eating the object (see forage above). Label all attention directed to the door of the night quarters building as manipulate. Record object of manipulation if possible.
P	Social **P**lay: one individual wrestles or gnaw-wrestles, plays chase games with, or leaps upon another animal in a context that is obviously nonagonistic. Typically accompanied by a play face; may be accompanied by quiet vocalization which is not recorded separately (see vocalize below). Do not use this code for instances of solitary play (see locomote and manipulate above). Record identity of play partner if possible.
Pr	**Pr**esent: one individual stands or crouches (usually quadrupedally) orienting the genital region toward another animal. Frequently followed by a genital inspection. Record receiver, if possible.
RD	**R**espond to **D**isplay: individual interrupts ongoing activity and orients toward display being performed by another individual (including noisy displays from inside building). May include, for example, running or climbing to get out of displayer's way, a simple head turn, and/or vocalization, which is not recorded separately (see vocalize, below).
RR	**R**egurgitation/**R**eingestion: animal regurgitates small amount of vomitus and reingests it. May be repeated several times per bout.
Scr	**Scr**atch: rough, long scratches of the animal's own body that produces a distinct rasping sound, frequently diagonally across the torso or up nearly the entire length of an arm. Very different from the light scratching performed within an autogroom.

Behavior	Definition
Sub	**Sub**mit/greet: individual behaves in a manner that acknowledges the higher social status of another animal by performing any of the following toward the subject: bared teeth face, bared teeth scream, bob, crouch, back-up, flee, pant grunt, or present (in a nonsexual context, see above). The category submit/greet should be used in lower intensity social encounters with another individual not involving a full display (see above). Contrast with respond to display (above). Record receiver of the submit/greet.
S	**S**tationary: individual is being passive and is not performing ANY of the other scoreable behaviors, i.e., contact close, etc. Usually consists of lying down, sitting, or standing while alone. Pauses for urinating or defecating will also be recorded here unless, or until, they result in coprophagy (see above).
V	**V**ocalize: individual produces a clearly audible sound that is not included within a behavior category described above. Indicate gradations with V+ for a loud vocalization, V- for a soft vocalization.
NV	**N**ot **V**isible: individual moves out of visual range during test period. If not visible for more than 1/4 of the test, repeat test.
Oth	**Oth**er: individual performs a behavior not described above, e.g., copulation, severe attack, etc. Always describe the nature of the "other" behavior on your data sheet.

APPENDIX D

APPENDIX D

IDENTIFICATION OF GORILLAS

Subject	Identification Description
1 Penney 	Adult female; born November 8, 1986 at GPZ; nursery reared; dam is Katanga, sire is Lamydoc. Has a great deal of light colored hair around her face (much like her mother), most in the form of "sideburns", and a lot of pale tan on her back and legs. Very heavy. Frequently makes faces and performs a characteristic "eye poke." Subject code: 4
2 Martha 	Adult female; born November 1, 1989 at GPZ; nursery reared; dam is Katanga, sire is Lamydoc. Mostly dark colored (beginning to lighten slightly along lower back and legs), long limbed, and relatively slender. Subject code: 7
3 Margaret 	Adolescent female: born December 18, 2007 at GPZ: dam is Martha and sire is Moja. Has a slightly squarer face and is overall a bit smaller than Samantha. Coat coloring is more contrasting from back and sides (lighter on lower back, darker across shoulders; almost like she is wearing overalls). Subject code: 22.
4 Mbundi 	Adult male; born January 12, 1993 at Calgary Zoo (but belongs to Toronto Zoo); transferred to Kansas City Zoo May 25, 1999; mother reared; dam is Tabitha; sire is Kakinga. Acquired by GPZ from Kansas City Zoo, November 19, 2014. Mature silverback, marked silvering across his shoulders and on lower back and thighs, a little smaller in stature than Lamydoc. The two silverbacks will never be displayed together, so there is little chance of confusing them. Subject code: 26.

BIOGRAPHICAL SKETCH

Claudia Martinez attended the University of Texas Pan American from 2009-2013, where she received her Bachelor of Science in Biology in December 2013. She then attended the University of Texas Rio Grande Valley from 2015-2020, where she received her Master of Arts in Psychology in May 2020. During her time there, she worked as a research assistant under the supervision of Dr. Valerie James-Aldridge, where she collected behavioral data on the western lowland gorillas at the Gladys Porter Zoo. She also instructed undergraduate students on how to collect and enter gorilla behavioral data. Both academically and personally, Martinez's fields of specialization are primatology and behavior analysis.

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