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Behavioral and Physiological Assessment of Zoo-Housed Heterosexual Gorilla (Gorilla gorilla gorilla) Troops with Multiple Silverbacks

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BEHAVIORAL AND PHYSIOLOGICAL ASSESSMENT OF ZOO-HOUSED HETEROSEXUAL GORILLA (*Gorilla gorilla gorilla*) TROOPS WITH MULTIPLE SILVERBACKS

by

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CERTIFICATE OF APPROVAL

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Abstract

Western lowland gorillas (*Gorilla gorilla gorilla*) are the only subspecies of gorilla housed in North American zoos. Based on recognized life history traits and ecology, zoos strive to house their gorillas in traditional family, or mixed-sex, groups with one silverback and multiple females. However, successful captive breeding programs and a nearly 50:50 birth sex ratio has created the need to house surplus males in solitary conditions and, more commonly, in all-male or bachelor groups. Although there are challenges associated with managing all-male groups in captivity, such groups have been observed in the wild and, compared to solitude, are deemed more appropriate for gorilla welfare. It is commonly believed that male western gorillas do not tolerate one another in the presence of females; however, such social structure has, albeit rarely, been observed in the wild. For this reason, some zoos have begun experimenting with this scenario. At the time of data collection, only four of the 51 institutions housing gorillas in the North American Species Survival Plan® population housed multi-male mixed sex groups. One of these groups was composed of two silverbacks less than 20 yoa. Of the three zoos that manage multi-male groups with two silverbacks older than 20 yoa, two were accredited by the Association of Zoos and Aquariums. Chapter one documents the activity budgets of two of these multi-male groups and compares them to behavior budgets of two traditional family troops. Overall behavior repertoire was similar between group type, though there were more frequent locomoting and aberrant behaviors in the multi-silverback groups. Interaction between the silverbacks varied greatly between the multi-male groups. The results suggest there could be multiple models of success for multi-male mixed-sex groups in zoological settings. However, further insight is needed to determine why some multi-male groups are successful with minimal intragroup silverback aggression while others are not. Therefore, the second chapter outlines the results of a multi-institutional survey which covered the recent history of multi-male mixed-sex groups in North American zoos. The goal of the survey was to determine factors associated with silverback compatibility. Results indicate that there is an association between successful multi-male mixed-sex groups and some life history factors including the relatedness of the males, their rearing histories, the time at which they were introduced, and their previous social experiences. This research offers insight into a potential gorilla social assemblage that has been underutilized in zoo settings.

Introduction

The western lowland gorilla (*Gorilla gorilla gorilla*) is one of the four subspecies of gorilla, the other three include the Cross-River gorilla (*Gorilla gorilla diehl*), the eastern lowland gorilla (*Gorilla beringei*), and the mountain gorilla (*Gorilla beringei beingei*). Although the western lowland gorilla's wild population abundance is the highest of the four subspecies at approximately 95,000 individuals, the species is still considered critically endangered (Walsh et al., 2008). This status was given by the International Union of Conservation of Nature in 2007 after western lowland gorillas experienced an 80% population decline over only three generations (Walsh et al., 2008). The main reasons for the continual reduction are commercial hunting, habitat destruction, and the Ebola virus (Walsh et al., 2008). In the 1950s, people began retrieving gorillas from the wild in an attempt to save and maintain their already declining numbers. By 1976 gorilla numbers were so low that they were inducted into the Appendix I of CITES. Thus, it became illegal to import them from the wild, and captive populations are now completely sustained through breeding programs (UNEP-WCMC, 2015). The threat of losing this species from the wild evokes a greater need to provide the best possible care for gorillas in human care.

In the wild, western lowland gorillas are predominantly found in family troops with one silverback, several females and their offspring (Parnell, 2002; Gatti et al., 2004). After dispersing from their natal group, males will remain solitary or sometimes join all-male or bachelor groups until they can find females of their own to lead (Gatti et al., 2003; 2004; Levrero, 2005; Parnell, 2002). On rare occasions, western lowlands have been observed forming multi-male heterosexual, or mixed-sex, groups (Parnell, 2002; Robbins et al., 2004). However, this structure is much more common in wild mountain gorilla troops, with 36-53% of mixed-sex groups having more than one silverback (Gray et al., 2010; Kalpers et al., 2003). The reason for the stark difference in the prevalence of multi-male mixed-sex groups between these two subspecies is still unknown, though researchers have made several speculations. For one, more mountain gorilla males tend to reside in their natal group upon reaching sexual maturity, and it has been shown that the male mountain gorillas who stay in their natal group have a higher reproductive success than those who leave (Robbins, 1995). However, despite the potential fitness benefits of staying within the natal group and forming multi-male groups, western lowland males generally disperse (Parnell, 2002; Stokes et al., 2003). Researchers have postulated this is most likely a result of the clumped resource distribution for western gorillas, as they are more frugivorous compared to the highly folivorous mountain gorillas (Parnell, 2002; Robbins, 1996).

Furthermore, it has been suggested that female mountain gorillas may prefer to disperse into multi-male groups as a means to lower the risk of infanticide to future offspring (Bradley et al., 2005), though mixed results on the matter have been reported (Watts, 2000; Robbins et al., 2014). Infanticide is a common occurrence during intergroup gorilla aggression, when an outside silverback takes over another silverback's troop (Breuer et al., 2010; Robbins et al., 2013). Rates of mountain gorilla infanticide have been shown to be higher in one-male groups when dominance tenures end compared to that of multi-male groups, generally due to the role of the second (or more) male(s) as a replacement leader (Robbins et al., 2013). There is greater variability in western lowland offspring survival compared to offspring survival of mountain gorillas (Robbins et al., 2014). This could be a result of the lack of natural predators for mountain gorillas or the higher prevalence of infanticide in western gorillas (Harcourt and Stewart 2007; Breuer et al. 2010; Robbins et al. 2013). However, as rates of infant mortality in western gorillas are similar to that of one-male mountain gorilla groups, some suggest these higher mortality rates are mainly due to higher rates of infanticide (Breuer et al. 2010). Even though western lowlands are not commonly found in multi-male groups, when multiple groups do associate, the males are known to show great tolerance of each other (Doran & McNeilage, 2001; Parnell, 2002). Thus, it seems possible that western lowland males could be compatible with each other given suitable conditions.

As previously stated, male gorillas have been known to form bachelor groups after natal dispersal; however, such groups are generally transitory and disband when the males find available females (Gatti et al., 2003; Parnell, 2002; Robbins, 1996). Because bachelor groups have been shown to be common transitional groups in the wild, the North American zoo-housed gorilla population is managed in a similar fashion. Surplus younger males are housed together in smaller groups; following maturity, some of these males are transferred to mixed-sex breeding groups (Stoinski et al., 2013). However, managing these bachelor groups has its challenges as there are higher rates of aggression and wounding associated with housing younger silverbacks together (Leeds et al., 2015; Stoinski et al., 2013). Thus, having additional housing options for these males could be beneficial for the zoo-housed population.

It is commonly believed that zoo-housed silverbacks will not tolerate each other in the presence of females, and higher wounding rates between males who have visual or olfactory access to females in zoo settings have been observed (Stoinski et al., 2004a). For this reason, the zoological community has had little experience attempting to manage multi-male mixed-sex groups. In 2016, in the North American Species Survival Plan® (SSP) gorilla population, there were three institutions, two accredited by the Association of Zoos and Aquariums (AZA), housing a mixed-sex group with two silverbacks over the age of twenty and one AZA accredited institution housing a mixed-sex group with two younger silverbacks.

As these zoos have shown, it is possible to house multiple Western Lowland males together with females, so it may be plausible to maintain at least a portion of zoo-housed males in mixed-sex groups. However, it is necessary to systematically assess such groups to determine the conditions in which they can thrive. Studies on zoo-housed males have shown that age is more of a determinant of behavior than group type (Leeds et al., 2015; Stoinski et al., 2013). Nevertheless, additional in-depth comparisons between traditional family troops and multi-silverback troops could help illuminate how such social settings impact the behavior of these apes. Chapter one investigates four zoo-housed mixed-sex troops to determine how and if an additional silverback affects group behavior. The overall behavior repertoire of two multi-male troops did not differ greatly from that of the single male troops, though the multi-male troops did engage in more aberrant and locomotive behaviors. Relationships among the silverbacks in each multi-male troop varied, as interactions were common in one pair and non-existent in the other.

Though some zoos have successfully housed multi-male mixed-sex troops, other institutions have attempted and failed to do so. Such occasion results in the necessary transfer of one or both males. If the zoo community could determine how to successfully house more males together in mixed-sex groups, it would create more opportunities for the surplus individuals. The second chapter assesses the gorilla SSP population's recent history of managing multi-male groups in an effort to determine if any ontogenetic or environmental factors may be associated with silverback compatibility. Similar to what has been suggested for successful bachelor group formation, this study determined age, relatedness, and rearing history to be factors associated with successful multi-male mixed-sex troops. Together, this work allowed for an in-depth look into the past and present management of multi-male troops and provided additional insight into a potentially underutilized management strategy for gorillas in human care.

Chapter 1

Activity budget comparisons between gorilla (*Gorilla gorilla gorilla*) multi-male heterosexual troops and traditional family troops with a look into the effects of an additional male on the fecal glucocorticoids of one multi-male troop

Abstract

North American zoos strive to house their western lowland gorillas (*Gorilla gorilla gorilla*) in heterosexual, or mixed-sex, groups with one silverback and multiple females. However, captive breeding programs and a nearly 50:50 birth ratio has created the need to house surplus males in solitary conditions or in all male/bachelor groups. In 2016, two of the 49 AZA accredited gorilla institutions manage a multi-silverback (>20 yoa) heterosexual group. This study evaluated the behavioral budgets and relationships of these troops housed at the Jacksonville Zoo and Gardens and the Franklin Park Zoo and compared them to those of two traditional family troops housed at Zoo Atlanta. Fecal glucocorticoids of one multi-male troop were also measured to determine whether the additional silverbacks were negatively impacting stress levels of group members. Aberrant and locomotive behaviors were higher in the multi-male troops, while all other behaviors were similar between groups. No interactions were observed between the silverbacks in one multi-male troop; however, aggressive interactions and displacements were common between the silverbacks in the second group. One silverback in each multi-male troop spent more time near females. Glucocorticoids levels differed between gorillas, yet no individual had elevated cortisol levels over the five-month sampling period. These results suggest multi-male mixed-sex groups can be successful in zoological settings. Moreover, there could be multiple models for the success in these groups.

Introduction

Gorillas (*Gorilla gorilla*) are a cognitive species that are known to form stable social groups. Wild groups usually consist of one mature male (or silverback), up to ten females, and their immature offspring, though some multi-silverback family units and all-male groups have been observed (Gatti et al., 2003; Magliocca et al., 1999; Parnell, 2002 Robbins et al., 2004). Multi-male heterosexual, or mixed-sex, groups are much less common in Western lowland gorillas (*Gorilla gorilla gorilla*) compared to mountain gorillas (*Gorilla beringei beingei;* Parnell, 2002; McNeilage et al., 2001). This difference is thought to be an effect of the western lowland females' propensity to join smaller groups which has been suggested to be related to the clumped resources and relatively higher intragroup feeding competition (Stokes et al., 2003). While western lowland females tend to join smaller groups, eastern mountain females, which live in more dietary rich areas, seem to show a preference for multi-silverback groups (Watts, 2000). Such is believed to be associated with a need to protect one's offspring. Specifically, single silverback groups are more likely to lead to group disintegration, where the death of the sole silverback results in the involuntary transference of his females to other groups (Parnell, 2002; Sicotte, 2001; Stokes et al., 2003). When females with infants attempt to join another group, the new silverback will sometimes kill the infant (Parnell, 2002; Watts, 1992; 2000). However, in multi-silverback groups, there is no need for the females to transfer into a new group if one male dies, because the other silverback(s) will still be present.

Western lowland gorillas are the most popular subspecies of gorilla to be housed in zoological institutions worldwide. At the time of publication, they were the only subspecies housed in North American zoos. When possible, zoos aim to house their gorillas in social groups similar to the majority of groups found in the wild. Such groups are known as heterosexual, or mixed-sex, family groups with one silverback and multiple females (Leeds et al., 2015; Stoinski et al., 2001b; 2013). Yet, with the success of zoo breeding programs, it is becoming harder to house all gorillas in human care in such groups. With an equal birth sex ratio, zoos have had to begin housing surplus males in solitary conditions or bachelor groups (Stoinski et al., 2004b). Of these two possibilities, bachelor groups are considered better for animal welfare, not only because such groups are known to occur in the wild, but they also provide the communal species with necessary social stimulation (Johnstone-Scott, 1988; Stoinski et al., 2002, 2004b.). In fact, the growing population has led researchers and zoo officials to estimate that within the next 30-50 years, all institutions housing gorillas will need to house both bachelor and family groups (Stoinski et al., 2004b). Creating and maintaining the necessary enclosures for the additional groups will have high monetary and human-power costs. To alleviate these costs, some zoos have attempted to house multiple males together in family settings. Though it is commonly suggested that western lowland silverbacks will not tolerate one another around females (Breuer et al., 2010; Robbins et al., 2004), family groups with multiple silverbacks have been observed in wild western lowland populations and are quite common in wild mountain gorillas (Parnell, 2002; Robbins et al., 2004). At the time of data collection, two of the 49 North American gorilla-housing institutions accredited by the Association of Zoos and Aquariums manage a mixed-sex group with more than one silverback (>20 yoa). Additional zoos have had success with similar management practices in the past while others have attempted and ultimately failed leading to the transfer one or more males due to escalating aggression. The zoo community could gain valuable insight by assessing the social dynamics and welfare of these successful multi-silverback mixed sex groups and the management practices of the zoos in which they reside. If more institutions could successfully house multiple silverbacks within breeding groups, it could potentially transform the future of gorilla management.

Behavioral observations have been used to monitor the welfare of animals in human care, and thus assess zoological management practices, for the past 30 years (Crockett & Ha, 2010). To date, there has not been an exhaustive study focusing solely on the behavioral dynamics of multiple silverbacks in mixed-sex groups, but comparative studies have found the behavior of males housed in bachelor and mixed-sex zoological groups to be similar (Stoinski et al., 2002; Stoinski et al., 2013). Age, rather than group type, seems to have more of an impact on behavior. Specifically, Stoinski et al. (2004a, 2013) found that affiliative interaction and close proximity rates are significantly higher in juvenile males, while non-contact aggression and display behaviors are exhibited more by silverbacks, with younger silverbacks (14 ≤ 20 yoa) engaging in the most aggressive behaviors. These age-related differences in the social behavior of males in human care are consistent with wild populations, in which males become less tolerant with age (Caillaud et al., 2008; Robbins, 1996). A positive linear relationship has also been noted between rates of non-contact aggression and the number of silverbacks in a group; this was the case for both all-male and mixed-sex groups (Stoinski et al., 2013). When examining only all-male groups, Stoinski et al. (2004a) determined that rates of non-contact aggression increase when the males are given visual or olfactory access to females. This conclusion coincides with findings from wild gorilla studies in which males in bachelor groups have stronger affiliative relationships than males in mixed-sex groups, which is believed to be a result of either the lack of females to form relationships with in bachelor groups or due to the competition and associated stress brought about by the presence of females in mixed-sex groups (Robbins, 1996; 2001).

Stress has been defined as the biological process used to cope with perceived threats (Broom & Johnson, 1993). Physiologically, the stress response occurs when the appearance of a trigger, or stressor, is detected by the brain. Such stressors induce a hormone cascade within the endocrine system which eventually results in the adrenal cortex releasing glucocorticoids. Inappropriate environments and social groupings can act as stressors for animals and can have negative consequences on their well-being, including suppressed reproductive and immune systems, increased stereotypic behavior, increased aggression, and increased cortisol levels (Aureli & de Waal, 1997; Burks et al., 2001; Kuhar et al., 2005). As such, stress should be considered and regularly monitored in zoological settings (Schwarzenberger, 2007).

One glucocorticoid, cortisol, is commonly used to indicate and measure stress in wild animals as well as those in human care (Wielebnowski et al., 2002). As with behavior, comparative studies have shown that glucocorticoid levels do not differ between males of bachelor and mixed-sex zoological groups (Stoinski et al., 2013). The same has been shown for wild males in such social groupings (Robbins, 1996). Although cortisol levels did not differ between the two types of social groups in zoological settings (bachelor and mixed-sex), Stoinski et al. (2002) did find urinary glucocorticoids were significantly higher in solitary males compared to males of either social structure. This finding suggests that solitary housing is more stressful and therefore a potentially less appropriate zoological management strategy. Also, similar to the observed behavior patterns, cortisol levels differed among age classes, with higher levels present in morning samples of juveniles than in samples of sub-adults and adults (Stoinski et al., 2002; Robbins & Czekala, 1997). Though cortisol expression is positively associated with stress levels, it can be correlated with other factors as well, including time of day, with higher expression in the morning hours (Coe & Levine, 1995; Stoinski et al., 2002; Sánchez et al., 2005), and increased physical activity (Perry & Gilmour, 1999; Girard & Garland, 2002; VanBruggen et al., 2011). As the juvenile males from the Stoinski et al. (2002) and Robbins and Czekala (1997) studies were rarely involved in aggressive interactions, the researchers believed their higher cortisol levels were more likely due to the increased activity levels of the younger animals than due to stress. To date, cortisol levels have been used to biologically validate behavioral measures indicative of stress in several species, including western lowland gorillas (Bettinger et al., 2001; Boinski et al., 1999; Cavigelli, 1999, Peel et al., 2005).

As care givers, it is our responsibility to constantly reassess and advance management practices to ensure we are providing the best possible environments for the animals in our care. It is possible that some of the surplus male gorillas, especially the solitary individuals, may not be living in optimal conditions. If the scientific zoo community could determine a successful way to incorporate surplus male gorillas into larger group settings, it could be beneficial to their well-being. However, empirical evidence is needed to ensure such environmental changes would indeed be advantageous for all troop members involved. The goal of this study was to empirically assess and learn more about a gorilla group structure that is uncommon in North American zoos to determine it has the capability to improve the welfare of surplus males. This aim was accomplished by (1) comparing the behavior patterns of two multi-silverback, mixed-sex groups to those of two traditional family groups to gain further information on group effects of additional silverbacks and (2) using simultaneously collected behavior and glucocorticoid data to outline appropriate measures of social stability and compatibility in one gorilla group.

Methods

Study Subjects

Subjects were 18 mature western lowland gorillas (*Gorilla gorilla gorilla*) residing in four social groups at three institutions (Table 1). Although there were juveniles and infants residing in these groups, data were only collected on individuals 10 years of age or older. Two of the four groups were traditional family groups, one with two females, the other with three females and each with one silverback. Both groups were housed in Zoo Atlanta (ZA). The other two groups were mixed-sex family groups, each with two silverbacks and three mature females. These groups were housed in Jacksonville Zoo and Gardens (JZG) and Franklin Park Zoo (FPZ) and were the only two multi-male mixed-sex gorilla groups housed in AZA accredited institutions at the time of data collection. Though these two multi-silverback groups had similar social structures, they were managed somewhat differently. The gorillas at JZG were housed together on exhibit each day. Overnight, they were either housed separately or in subgroups depending on individual compatibility. A third silverback also resided at FPZ, but he was not compatible with the other two males. Thus, this zoo employed a rotational system in which the females were exhibited with the one silverback on one day and housed with the two compatible silverbacks on the next day. On the days that the silverbacks were not on exhibit, they were maintained in their respective holding areas. Overnight, the females were housed together while each male resided in their individual night rooms.

Data Collection

Behavior observations took place between the months of October 2016 and April 2017. Observations of the JZG and FPZ groups were conducted using the same ethogram and data collection methods. The primary investigator and three assistants, two at JZG and one at FPZ, conducted these observations. The assistants met an inter-observer reliability criterion of at least 85% agreement with the PI before collection began. Data from ZA, however, were collected as part of separate, ongoing behavioral observations. Therefore, the data output had to be modified to better reflect those of the PI's ethogram and collection methods. This modification process is outlined in greater detail below.

At JZG and FPZ, the gorillas were observed for at least one 1 hr session each observation day, between 9:30am and 2:00pm. JZG observations occurred up to four times weekly resulting in a total of 78 hr. Due to decreased observer availability and feasibility, FPZ observations occurred one to two times a week and resulted in 22 observational hr. At the start of each observation session, the number of visitors present at the exhibit was recorded using one of three categories (zero= zero visitors, one= ≤ 15 visitors, two= 16 - 39 visitors, three = ≥ 40 visitors). Individual gorilla behavior was recorded using group scan and all occurrence sampling methods (Altmann, 1974; Crockett & Ha, 2010). All predefined behaviors (Table 2) for each adult gorilla were recorded at 5 min intervals throughout each session. As each scan behavior was noted, the proximity of all individuals was also recorded (Table 3). Because the ethogram categories were not mutually exclusive, a behavioral hierarchy was used to determine which behavior was recorded if two or more behaviors occurred concurrently (Figure 1). Social interactions and aberrant behaviors involving a male were treated as all-occurrence behaviors and were noted even if they occurred outside the recording period, while all other behaviors were only noted at the five-minute intervals. A modifier of each social behavior, representing other individuals involved in the interaction, was recorded when appropriate. Although data were not collected on infants, they still acted as modifiers. The ZooMonitor iPad app was used for all behavior data collection (Ross et al., 2016). The location of each individual within their respective enclosures was recorded at 12 min intervals. The 12-min interval was chosen because this interval would not overlap with behavior coding scans and would still allow an adequate number of location points each session. This app allowed the visual depiction and evaluation of exhibit occupancy maps.

Data from ZA were part of an ongoing behavioral monitoring program. These data were collected in 10 min sessions using focal sampling and sequential activity recording methods (Atlmann, 1974). The target behaviors were similar to those in the ethogram used for JZG and FPZ data collection. See Hoff, Hoff, and Maple (1998) for the ZA ethogram and data collection procedures. To allow for better behavior budget comparisons between the four gorilla groups, the ZA data outputs were adjusted so that only behaviors occurring at the 1 min, 5 min, and 10 min time points of each session were used. The sequential behaviors of the ZA silverbacks were also compared to the all-occurrence behaviors of the JZG and FPZ silverbacks. Data from Zoo Atlanta was collected from October 2015 to March 2016 and, to account for potential seasonal variation, October 2016 to March 2017. Such sampling resulted in approximately 15 hours of observation per ZA gorilla.

Behavioral Data Analysis

All out-of-view scores were removed for each individual. The percent of time each animal spent in view was calculated using scan data. Then, using the scan data, mean percent of time spent in each behavior was calculated for each adult animal. This measurement was used to determine the rate per visible hour the animals spent in each all-occurrence behavior (Stoinski et al., 2004a). The scan and all-occurrence behaviors were compared between the four groups using a linear mixed model. Due to potential confounding effects between zoological institutions, this was added into the models as a covariate for all behavioral analyses. When needed, non-parametric testing equivalents were used. Because the interval data did not meet the assumptions of a normal distribution and homogeneity of variance, these behaviors were analyzed using the non-parametric version of an ANCOVA, Quade's Rank (1967) test. Parametric ANCOVA was used to assess patterns in the all-occurrence data. These models were employed to assess effects of group type on behavior. This type of analysis allowed for the control of individual differences between subjects and zoos. All analyses were conducted using SPSS version 24.0 at an alpha of 0.05 (IBM Corp, 2016).

The directionality of social behaviors was determined for the silverbacks via an index of asymmetry (Robbins, 1996; Stoinski et al., 2004b). This index followed the equation $Z=(X-Y)/(X+Y)$, in which X represents the number of times the silverback initiated the social behavior with another, and Y is the number of times a conspecific initiated the social behavior with the silverback. The resulting Z numbers could range between 1 and -1. Positive Z numbers indicated the silverback initiated the social interaction more, while negative numbers meant the conspecific was more likely to seek interaction. The magnitude of the Z numbers revealed the degree at which the silverback initiated interactions over the conspecific. Thus, Z scores closer to 0 indicated more equal initiation from both individuals and scores closer to -1 or 1 revealed one-sided social interactions.

Space-use Analysis

Using ZooMonitor, the enclosure was divided into six quadrants and the Spread of Participation Index (SPI) was used to quantify exhibit-use for each adult gorilla. The SPI, as represented by the equation below, used the frequencies of observations in each quadrant to determine the degree to which each gorilla used their allotted space (Dickens, 1955; Ross et al., 2011a).

$$SPI = M * (Nb - Na) + (Fa - Fb) / (2(N - M))$$

In this equation, M represents the mean frequency of observations in all quadrants; Nb is the number of quadrants below this mean; Na is the number of quadrants above the mean; Fa is the number of observations within Na, Fb is the number of observations within Nb, and N was the total number of observations for that gorilla. Such calculations resulted in a SPI score for each adult gorilla. The score could range from 0 to 1; scores near 0 indicated total enclosure use, in which all quadrants were used equally, while those closer to 1 indicated minimal overall space use, in which the animal used only a few quadrants.

Fecal glucocorticoid analysis

Fecal cortisol levels were assessed in conjunction with the behavioral data from JZG. A minimum of two morning fecal samples from each mature gorilla were collected every week for 4.5 months, resulting in 41 to 42 samples per individual. Not all gorillas were housed separately overnight. For this reason, edible colored dye was administered into the diets of the gorillas (Fuller et al., 2011). Each individual was assigned a different color of dye to help distinguish their feces. All urine and substrate contaminated feces were discarded. Samples were stored at -20°C within two hours of collection (Washburn & Millspaugh, 2002). The samples were driven to the University of North Florida SEZARC laboratory at the end of the study.

Glucocorticoid Extraction Process

Approximately 0.50g of each thawed sample was weighed and added to 16x100mm extraction tubes. To extract the fecal cortisol metabolites, 1 mL of RO water and 4 mL of 100% methanol were added to each tube (Metrione et al., 2008). After being shaken for 15 min, the tubes were centrifuged for 10 min at 3100 rpm. Next, 500µL of the supernatant was removed from each tube and placed into separate 12mm x 75mm tubes. These samples were left uncapped for four days, so the supernatant would evaporate. Dried samples were then shipped to Dr. Rupert Palme at the University of Veterinary Medicine, Department of Biomedical Sciences in Vienna, Austria to be analyzed.

Enzyme immunoassay and data analyses

Cortisol was quantified using a validated competitive enzyme immunoassay against 5-reduced cortisol metabolites with a 3alpha, 11beta-dihydroxy-CM structure. This assay has been shown to detect adrenocortical activity in western lowland gorillas. Furthermore, compared to similar assays, it has been determined to be most suitable for monitoring fecal glucocorticoid metabolite output in gorillas as it measured the highest levels of metabolites and displayed the strongest response to known stressors (Shutt et al., 2012).

Statistical Analysis

Gut lag-time in apes has been determined to be between 24 to 48 hours (Bahr et al., 2000; Peel et al., 2005), thus remaining analyses were conducted with a one to two-day lag time between observed behaviors and determined fecal cortisol levels. Behavioral profiles and glucocorticoids were assessed using Spearman's rho correlation to determine potential relationships between behaviors and fecal cortisol concentration. Six fecal samples dates were excluded from the correlation analyses because they fell outside the one to two-day lag time for observation days. Thus, 36 of the 42 samples for each gorilla were used for these analyses. As rates of aggression have been shown to induce higher cortisol levels (Muller & Wrangham, 2004), known aggressive bouts, revealed by the collected data and extensive animal care notes of gorilla keepers, were compared against associated cortisol levels via binary logistic regression models to determine whether aggression was a significant predictor of elevated fecal cortisol. All 42 samples were used in these analyses for four of the five gorillas. One female had one abnormally large cortisol peak due to a non-gorilla induced injury occurring to her infant, so that outlier was thrown out for all of her analyses; one male was missing a sample due to the inability of keepers to collect a fecal sample for that sampling period. Hormone concentrations are expressed as ng cortisol mass per g of feces (ng/g).

Results

Behavior Comparisons

Quade's Rank tests determined the exhibition of two scan behaviors to be statistically different between the two group types (Table 4). On average mature gorillas in multi-silverback groups spent more time locomoting ($F_{1,17}$=4.760, p=0.047) and exhibiting abnormal behaviors ($F_{1,17}$=5.302, p=0.038). As parametric testing was appropriate for the all-occurrence data, the social interactions and abnormal behaviors of the silverbacks were compared via subsequent ANCOVA (Table 5). Analyses determined that the average amount of time spent engaging in aggressive behaviors per visible hour was statistically higher for the silverbacks in multi-silverback groups ($F_{1,5}$=35.619, p=0.009, $F_{1,5}$=18.927, p=0.022). Gorillas in multi-male groups also displaced others more frequently ($F_{1,5}$=38.190, p=0.008). These interactions include those directed towards females, juveniles, and other silverbacks. It should be noted that throughout the 78 hours, no interaction was observed between the JZG silverbacks, and they were never within 2 m of each other. Interaction between the FPZ silverbacks was observed; however, none of this interaction was affiliative in nature. When removing the aggression and displacement interactions that these silverbacks directed toward each other, the group effect was no longer significant (Table 6).

Furthermore, though displacements did not differ statistically between group types after accounting for such male on male interactions (Table 6), there were differences between the average percent of time each silverback spent displacing a conspecific r or being displaced by a conspecific. Out of all silverbacks, those at FPZ had the highest frequencies for displacing conspecifics, while those at JZG had some of the lowest frequencies. Additionally, only the JZG silverbacks were observed ever being displaced by females (Figure 2).

The differences in displacement frequency was also illustrated in the calculated indices of asymmetry for social interactions (Table 7). The Z scores in this index represent the direction and magnitude of the overall social behaviors of each silverback. For displacements, the Z scores for the ZA and FPZ silverbacks are one. As Z-scores range from -1 to 1, and positive numbers indicate most of interactions are initiated by the silverback, their scores of one reveal these silverbacks' displacements were completely one sided: they displaced others and were never displaced themselves. Conversely, both JZG silverbacks have negative Z scores for such interactions, illustrating that they were displaced more than they displaced others. The Z scores for the other social interactions revealed some differences between the silverbacks' individual interaction initiation patterns, but, aside for displacements Z scores, no other overall trends were observed between group types.

Additional proximity analyses determined that group type did not have a statistical effect on the amount of time a silverback spent near or touching a conspecific (Table 8). However, data indicated that one silverback from each multi-male troop did spend more time near females than the other one (Figure 3). Separate proximity analyses for the females revealed that females in multi-male groups tended to spend more time proximate to another mature gorilla than females in traditional family groups ($F_{1,11}$=6.630, p=0.030, Table 8).

Space Use

There number of visible location scans for the JZG gorillas ranged from 407 to 422 scans. Due to the decreased observer availability, the average visible scans for the FPZ gorillas was lower at 55 scans. The generated space-use images and accompanying SPI scores did reveal differences in the way each gorilla used their allotted area. At JZG, the two silverbacks had the highest SPI scores, indicating that they were using minimal enclosure space (Table 9). Moreover, these males were using space opposite of each other; one remaining in the north end of the enclosure and the other in the south end (Figure 4). Compared to the silverbacks, the females utilized more of their exhibit space, though still not evenly (Figure 5). The SPI scores of the FPZ silverbacks were considerably lower than those at JZG (Table 9). Though this could be an artifact of the small sample size, the caregivers at the institution maintain these data reflect what they observe on a daily basis. The space-use images suggest these males were moving around their space more evenly (Figure 6), and the gender difference between space-utilization at FPZ were less apparent than that at JZG (Figure 7).

Fecal Glucocorticoids of JZG Gorillas

Cortisol levels ranged from 63.09 ng/g to 1060.79 ng/g with highly variable individual averages (Table 10). Calculated standard deviations revealed that within individual variation was similar for the five gorillas (Table 10). There was no apparent gender relationship, as one silverback had the highest cortisol levels of the group and the other had one of the lowest. Individuals' outliers were defined as samples that were greater or less than two standard deviations from their mean (Schmidt-Reinwald et al., 1999). None of the gorillas had low outliers; however, they all had at least one high outlier (Table 10). Overall hormonal profiles did not reveal any pronounced time during the sampling period in which all gorillas had sustained higher-than-baseline cortisol levels (Figure 8). Furthermore, binary logistic regression models did not indicate a predictive relationship between aggression and elevated cortisol levels for any of the five gorillas (Table 11). However, there were significant correlations between cortisol levels and solitary behaviors and/or proximity states for three of the individuals. Bulera's data suggested that there was a positive correlation between her cortisol levels and the amount of time she spent in proximity to a conspecific ($r_s(35)= -0.336$, $p=0.048$) and the amount of time she spent locomoting ($r_s(35)=0.440$, $p=0.008$; Figure 9). There was a negative relationship between Rumpel's cortisol level and the amount of time he spent inactive ($r_s(36)=-0.537$, $p=0.001$; Figure 10). Madini's results revealed a positive correlation between the amount of time she spent distant, or more than 2 m from another conspecific, and her cortisol levels ($r_s(36)=-0.336$, $p=0.045$; Figure 11).

Discussion

Behavioral Measurements

The overall behavioral comparisons between all troop members revealed that locomotion and aberrant behaviors were both higher in multi-male troops compared to traditional family troops. Average frequency of locomotion for wild western gorillas has been demonstrated to be between 12% and 22% of the animals' overall recorded budget (Remis, 1994; Magliocca & Gautier-Hion, 2002; Masi et al., 2009; Klailova, 2011). However, locomotion rates for gorillas in human care are commonly shown to range from 5% to 14% of their overall budget (Hoff et al., 1996; Hoff et al., 1997; Lukas et al., 2003; Bonnie et al., 2016). Because most of the locomotion observed in wild populations is the result of necessary travel between clumped fruiting resources (Masi et al., 2009), locomotion would be expected to be lower in zoological settings where provisions are offered in closer proximity to the apes. Although the observed locomotion frequencies in this study, 18% for multi-male groups and 12% for traditional groups, were determined to be significantly different, both frequencies were within the known ranges for this species. As there is yet an established optimum target activity level for this species (Ross et al., 2011b), it would be impossible to implicate any differences in welfare based solely on this behavioral difference.

Conversely, elevated frequencies of aberrant behaviors have commonly been used as a proxy for welfare in zoological animals (Marriner & Drickamer, 1994; Novak et al., 2006; Mason et al., 2007). The cause of aberrant behaviors or stereotypies in zoo settings is largely debated, though the exhibition of these behaviors in primates has been linked to rearing history, exhibit design, disruption in social structure, and diet (Maple & Finlay 1986; Marriner & Drickamer, 1994; Lukas, 1999; Lukas et al., 2010; Ross et al., 2011b). As the observed rate of aberrant behaviors in the multi-male groups was approximately 11%, nearly ten times that of the traditional family group at 1.5%, the results may appear to imply overall decreased welfare for the multi-male troops. However, the exhibition of aberrant behaviors in gorillas is known to vary drastically between individuals (Lukas, 1999; Stoinski et al., 2012; Greco et al., 2016), and the high standard error of the mean for the multi-silverback group could reveal the same trend in this population. Moreover, it is necessary to consider additional potential factors for this higher rate. For instance, studies have indicated that hand-reared apes are more likely to exhibit aberrant behaviors compared to those reared by parents or species-appropriate surrogates (Marriner & Drickamer, 1994; Jacobson et al., 2016; Zhang, 2017). Seven of the ten gorillas housed in the multi-male groups for this analysis were hand-reared, while all eight from the traditional group were parent-reared. Although it is possible that the observed elevated frequency could be an artifact of the additional male, the small sample size makes it difficult to confirm. Thus, this finding will need to be thoroughly considered until additional multi-male groups can be assessed.

Silverback Relationships

Based on data of male interactions in wild mountain gorilla multi-silverback troops, the higher levels of observed interaction between the two FPZ silverbacks is somewhat of an anomaly. Similar to what was observed at JZG, wild intragroup silverback interaction is rare and is only observed during intergroup encounters when the males are forced to work together to ward off mutual threats and prevent female emigration (Watts, 1995; Robbins, 1996). Interaction rates are often so low that researchers have postulated that silverbacks in multi-male mixed-sex groups actively avoid each other to maintain low levels of intragroup aggression (Robbins, 1996). As outside threats are non-existent in zoological settings, silverbacks would not need to form such coalitions, thus the lack of apparent relationship between the JZG silverbacks could be indicative of this active avoidance. The higher frequency of interaction observed between the silverbacks at FPZ may be a result of their past experiences. These two males have been housed together since they were four years of age, while the JZG silverbacks were introduced to each other during their twenties. Therefore, the FPZ males may be more willing to engage in interaction because they are more comfortable with each other (Robbins, 1996). Conversely, it is possible that the high rates of aggressive interactions between these males could be suggesting a growing tension between the pair that may lead to their eventual separation. Stoinski and colleagues determined increased non-contact aggression was a function of the number of males in the group (2013). Even though their analyses included males from bachelor groups, the aggressive interactions between the FPZ silverbacks could be mirroring their findings. This positive relationship between aggression and the number of males as well as the existence of fewer opportunities for males to avoid each other in zoo enclosures has led to the assumption that multi-male mixed-sex groups may not be feasible in zoo settings (Stoinski et al, 2004b). However, wild western lowland males show great tolerance of each other when groups come together, greater tolerance than is even observed in male mountain gorillas (Parnell, 2002). Thus, zoo-housed multi-male groups may be able to succeed given appropriate space and conditions, as has been demonstrated by the JZG and FPZ troops.

In both multi-male troops, the percentage of scans in proximity of a female was higher for one silverback compared to the other. Such proximity pattern is similar to what has been observed in wild mountain gorilla multi-male troops where females tend to congregate around one or two males while the other male(s) remain in the periphery of the group (Robbins et al., 2005; Rosenbaum et al., 2016). Females in multi-male groups even compete with each for proximity to one of the silverbacks (Watts, 1992). In the wild, the preferred silverback is usually the dominant individual (Stewart, 2001; Rosenbaum et al., 2011). However, dominance between males was difficult to measure in this analysis, as the males never interacted with each other to demonstrate dominance or their interactions were evenly matched (Robbins, 1996). Thus, it is difficult to determine the underlying mechanism of female preference in these populations.

Dominance and the Control Role

As silverbacks are typically the dominant troop figure, they are known to maintain a control role within their group (Hoff et al., 1982; Fossey, 1983; Watts, 2000; Margulis et al., 2003; Harcourt & Stewart, 2007; Less et al., 2010; Klailova, 2011). Such is certainly the case for wild western lowland and mountain gorilla populations where the loss of the silverback leads to group disbandment (Robbins, 1995; Stokes et al., 2003; Harcourt & Stewart, 2007). Moreover, several studies of zoological populations have determined that troop integrity is dependent upon the presence of the silverback. With the loss of a dominant silverback, the social dynamic of the group will destabilize resulting in increased aggression, increased abnormal behaviors, decreased feeding time, and decreased affiliative interaction (Hoff et al., 1982; Hoff et al., 1998; Margulis et al., 2003; Less et al., 2010). Overall, his dominance is demonstrated in his ability to maintain order and resolve disputes within the groups (Hoff et al., 1982; Watts, 1992; Robbins, 1995). Dominance rank in primates has often been measured by the number of displacements an animal can induce in proportion to the number of times they themselves are displaced (Stoinski et al., 2001b; Robbins et al., 2005; Robbins, 2008; Wright et al., 2014). Based on this measurement, both traditional silverbacks and the two FPZ would be dominant over the females in their group. Interestingly, as the behavioral data and accompanying z-scores demonstrated, both JZG silverbacks were displaced more often by their females than they displaced the females. Also, personal observations from the study revealed the silverbacks were not likely to fully intervene in female disputes. This could indicate that the females may not view these silverbacks as the dominant individuals within the troop. Even so, aggression levels for this group were not pointedly higher than those of the other three groups. While this seemingly goes against the control role theory, it is possible that this lack of male dominance is what allows this specific multi-silverback group to function, as neither male is attempting to exert dominance over the other.

Space-use

The high SPI values and accompanying space-use illustrations for the JZG silverbacks seem to support the notion that these males are actively avoiding each other. However, it cannot be assumed that they were residing in different areas of their enclosure solely due to the presence of the other male. In fact, gorillas often show some degree of space-use preference (Ogden et al., 1993; Steel et al., 1994; Stoinski et al., 2001a; Ross & Lukas, 2006). Stoinski and colleagues (2001a) assessed space-use on 19 gorillas housed at Zoo Atlanta, seven of which were subjects for this present study. They concluded that the gorillas spent 50% of their time in less than 15% of their allotted exhibit space. Moreover, both males and females were less likely to spend time in open-areas and preferred to remain in corners or along walls. Ross and Lukas had similar findings in 2006. The 14 gorillas in their study also showed preferences for corners, and an even stronger preference for space adjacent to mesh barriers to keeper areas. As depicted in the space-use maps, the north side of the enclosure in which Rumpel remained was near a keeper training window and the gorilla holding building. It is likely that Rumpel chose to remain here because it was a corner, close to keeper interaction, and close to the entry and exit points of the holding building (Ross & Lukas, 2006). Lash's preference for the south side of the exhibit is harder to speculate. It contained a corner which may provide a sense of protection (Ross & Lukas, 2006), and there was a training window nearby; however, it was rarely used. The fact that this area was the farthest from the holding building and the training window by which the other gorillas were commonly fed, suggests social factors likely influenced Lash's space utilization.

Fecal Glucocorticoids

The determined glucocorticoid levels are similar to the range of the baseline levels from a previous study on zoo-housed western lowland gorillas which used the same enzyme immunoassay (Shutt et al., 2012). However, the assay from the previous study was not conducted in the same lab as the current assay, and as these assays are exceptionally sensitive to environmental conditions, comparisons between studies are usually inappropriate unless the environmental preparation conditions are held constant (Heistermann et al., 2006.). Thus, such analyses are more suitably used when results are compared within your specific study population. Given this, the analyses suggest that the multi-male group was not overtly stressful for any individual in the group as no animal's levels were consistently elevated. It is possible that Lash's higher average was the result of a perceived threat or induced stress caused by Rumpel's appearance; however, such cannot be exclusively determined as elevated cortisol has been associated with factors relative to Lash's personal history including old-age (Lupien et al., 1998) and cardiovascular disease (Whitworth et al., 2005). Heart disease in common in the zoo-housed gorillas, especially older males (Kenny et al., 1994; Krynak et al., 2017). At the time of the study, Lash was 40 years old and the oldest gorilla in his troop. He has also had a history of heart-related illness. Given this, a direct correlation between Lash's high cortisol levels and the presence of an additional silverback is not possible to conclude.

The correlation rank results indicated Rumpel's cortisol levels were inversely related to his frequency of inactivity. Though inactivity has been considered problematic by those in the animal care field (Stevenson, 1983), there could be certain instances when lower levels of activity would be indicative of a calm, content animal (Ross et al., 2011b). Such theory is supported by the fact that inactivity is a mutually exclusive behavior, and thus could be replacing the potential expression of bouts of aggression or aberrant behaviors. A similar conclusion can be drawn for Bulera, as the correlation analysis revealed her cortisol levels were higher when she exhibited higher frequencies of locomotion. Both Bulera and Madini's correlation results suggest their cortisol levels were lower when they were closer to conspecifics. Female gorillas are social beings and are believed to feel most comfortable and safe when near a troop member, specifically the dominant male (Watts, 1992; Rosenbaum et al., 2016). Additionally, the females' proximity to their infants were included in these analyses as well. The social bond within gorilla mother-infant pairs is immensely strong (Maestripieri et al., 2002; Nowell & Fletcher, 2007;

Eckardt et al., 2016), and they often remain in close proximity to each other throughout the offspring's sub adulthood (Nowell & Fletcher, 2007). Thus, the results may be indicating elevated stress levels of the mother when they are farther from their infants.

Four of the eight cortisol outliers could be explained by potentially stressful environmental occurrences. Lash's highest outlier was 1061 ng/g from December 21, 2016. Daily social reports recorded by the keepers revealed that a major altercation occurred two days prior on December 19th. This altercation involved multiple contact aggression bouts between the three females in which Lash attempted to intervene but was unsuccessful. As previously indicated, Bulera's outlier of 1186 ng/g on February 11, 2017 can be explained by an incident that occurred with her son Densi on February 9th wherein he broke off an electrical cord from one of the enclosure fans and may have received a small shock from the disconnected wiring. One of Madini's outliers was 685 ng/g and occurred on January 11, 2017. Keeper records indicated that a physical altercation occurred between Madini and Kumbuka on January 9th. Though there were several aggressive interactions between these two gorillas throughout the observation period, but this specific incidence separated Madini from her daughter, Merah, who was stress vocalizing. Lastly, one of Kumbuka's outliers measured 591 ng/g on February 1, 2017 and occurred two days after a noted physical altercation between her and Lash. Neither the recorded behavioral data or keeper notes provided any substantial reasoning for the other four observed outliers. However, the observed relationships between the stressful incidences and elevated cortisol levels depicted above add additional validation the results of the immune enzyme assay and provide support for the use of fecal glucocorticoid monitoring in zoo-settings.

Conclusions

The data collected from these four groups indicated that the number of males in mixed-sex groups did not have major impacts on overall troop behavior. Behavioral and endocrinological measurements of one multi-male troop seemed to reveal that troop members were not suffering any negative effects from the multi-male structure; however, assessments from additional multi-male groups would be necessary to validate this conclusion. The drastic differences in the frequency of interaction between the silverbacks in each group suggests there could be multiple models for successful multi-male groups in zoological settings. In moving forward with this assumption, it would be necessary to monitor each potential group independently, as what works for one group may not work for another. Further analyses are needed to determine why some multi-male groups are successful with minimal intragroup silverback aggression while others are not. As with any social dynamic, multiple factors most likely play a role in the probability of silverback compatibility (Chapter 2).

Acknowledgements

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Table 1. Gorilla group composition and life history traits.

Name	Sex	Date of Birth	Birth/Rearing History	Institution
Lash	M	12/1976	Captive/Hand	**Jacksonville**
Rumpel	M	08/1984	Captive/Hand	
Bulera	F	01/1989	Captive/Hand	
Densi	*M*	*02/2015*	*Captive/Parent*	
Madini	F	06/1996	Captive/Parent	
Merah	*F*	*05/2015*	*Captive/Parent*	
Kumbuka	F	08/1996	Captive/Parent	
Okpara	M	07/1993	Captive/Hand	**Franklin Park**
Little Joe	M	02/1993	Captive/Hand	
Gigi	F	07/1972	Captive/Hand	
Kiki	F	08/1981	Captive/Hand	
Azize	*F*	*05/2015*	*Captive/Parent*	
Kambiri	*F*	*11/2010*	*Captive/Parent*	
Kimani	F	11/2004	Captive/Parent	
Ozoum	M	~1961	Wild/Parent	Zoo Atlanta
Choomba	F	~1963	Wild/Parent	
Shamba	F	~1959	Wild/Parent	
Taz	M	07/1989	Captive/Parent	Zoo Atlanta
Kuchi	F	10/1984	Captive/Parent	
Henry	*M*	*5/2010*	*Captive/Parent*	
Kudzoo	F	02/1994	Captive/Parent	
Merry Leigh	*F*	*08/2011*	*Captive/Parent*	
Sukari	F	05/1998	Captive/Parent	
Anaka	*F*	*08/2013*	*Captive/Parent*	
Lulu	F	08/1999	Captive/Parent	
Andi	*F*	*03/2013*	*Captive/Parent*	

*Infants and juveniles are italicized and indented under their mother. These individuals were not used as focal subjects but were included as social modifiers. In the *Birth/Rearing History* column, 'Wild' and 'Captive' signifies their origin of birth; 'Hand' indicates they were human raised for at least the first 6 months of their life, while 'Parent' indicates they were raised by their gorilla mother.

Table 2. Behavioral definitions of the condensed ethogram - modified from Stoinski et al., 2004a

Behavior	Modifier	Definition
Affiliative	Partner	Subject engages in a positive, non-agonistic interaction with another individual, including grooming, playing, etc.
Aggressive	Partner	Subject directs agonistic social behaviors toward another individual, divided into non-contact and contact interactions
Displace	Partner	Subject exhibits clear instances of displacement, avoidance, crouchin etc.
Aberrant	None	Subject exhibits any species atypical behaviors, including regurgitation and re-ingestion, self-injurious behaviors, coprophagy, repetitive movement and hair plucking
Locomotion	None	Subject is moving in a horizontal or vertical plane
Forage	None	Subject is searching for or ingesting the daily diet, includes drinking
Object	None	Subject actively manipulates a temporary or permanent (non-food) item within the enclosure
Self	None	Subject exhibits self-directed behaviors including auto-grooming, scratching, rubbing, etc.
Inactive	None	Subject is not moving or participating in any of the above behaviors, eyes can be open or closed

*Male social behaviors as well as male aberrant and display behaviors (italicized) were treated as both scan and all-occurrence behaviors. Though reproductive behaviors were in the initial ethogram, no such behaviors were observed, so they were not included in the analyses.

Table 3. Categories for proximity indication- modified from Ross et al., 2011b

Proximity	Modifier	Definition
Contact	Contact Individual(s)	Subject is touching another individual
Proximate	Neighbor(s)	Subject is within 2 m of another
Distant	None	Subject is more than 2 m of another
Proximate adult (contact infant)	Neighbor(s)	Only for mothers- if in contact with own infant and within 2 m of another individual
Contact adult (contact infant)	Contact Individual(s)	Only for mothers-if in contact with own infant and in contact with another individual
Unknown	None	Subject or possible neighbors are obstructed from view

* Only proximity to fellow adults were used for mothers in all behavior-only analyses, while their proximity to infants was used in the behavior and cortisol correlation analyses.

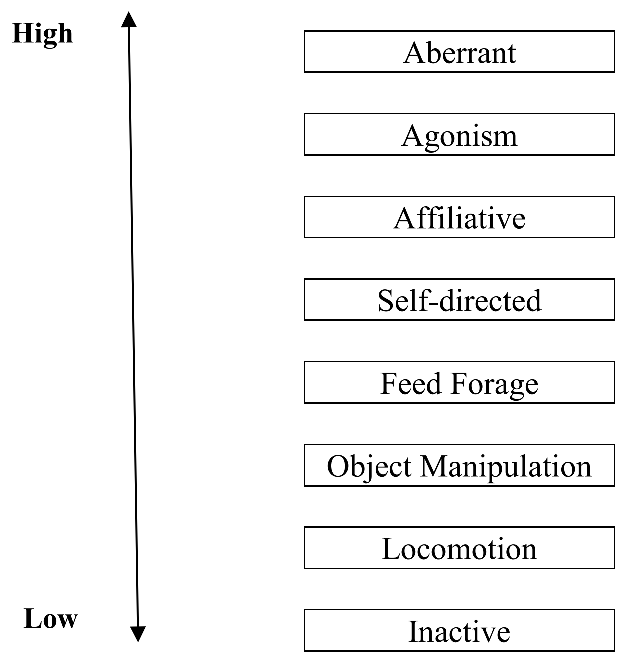


Figure 1: Behavioral hierarchy used with the non-mutually exclusive ethogram. When more than one behavior occurred concurrently, the highest ranked behavior was recorded.

Table 4: Comparison of the average percentages (SE) of mature western lowland gorilla behaviors observed in two group structures: multi-silverback mixed sex troops (n=10) and traditional family troops (n=8). Values are shown as the average of the gorillas' percentage of overall activity budgets spent in each behavior as depicted by five-minute interval scans.

	Mean Percent (SE)			
Behavior	**Multi-Silverback**	**Traditional Family**	**F**	***p***
Inactive	42.318 (6.820)	40.419 (3.616)	5.014	0.071
Forage	23.424 (4.415)	25.292 (2.005)	0.007	0.936
Locomotion	18.831 (4.143)	12.647 (1.892)	4.760	*0.047
Aberrant	11.03 (6.287)	1.474 (0.923)	5.302	*0.038
Self	5.093 (2.849)	6.095 (0.764)	4.450	0.075
Object	3.133 (0.784)	0.5868 (0.266)	0.192	0.668
Receive Affiliation	1.327 (0.423)	4.331 (1.367)	1.045	0.374
Initiate Affiliation	0.595 (0.239)	0.375 (0.125)	0.196	0.665
Receive Aggression	0.443 (0.254)	2.318 (2.211)	0.085	0.775
Initiate Aggression	0.480 (0.220)	0.389 (0.236)	0.151	0.703
Displace Another	0.190 (0.161)	3.299 (1.549)	3.808	0.079
Displaced by Another	0.256 (0.179)	0.675 (0.275)	2.918	0.115

* $p < 0.05$

Table 5: Comparison of the average percentages (SE) of silverback behaviors observed in two group structures: multi-silverback mixed sex troops (n=4) and traditional family troops (n=2). Values are shown as the average of the gorillas' percentage of time spent exhibiting the behavior per visible hour. This table encompasses all interactions observed throughout the study, including those between the silverbacks themselves.

	Mean Percent (SE)			
Behavior	**Multi-Silverback**	**Traditional Family**	**F**	***P***
Aberrant	4.968 (2.407)	0.937 (0.937)	0.158	0.717
Receive Affiliation	0.9649 (0.551)	3.8853 (3.48974)	0.586	0.500
Initiate Affiliation	0.7607 (0.305)	1.7517 (1.68579)	0.064	0.817
Receive Aggression	0.6974 (0.333)	0.0625 (0.06250)	35.619	*0.009
Initiate Aggression	0.874 (0.379)	0.4080 (0.34204)	18.927	*0.022
Displace Another	1.0591 (0.549)	0.3750 (0.375)	38.190	*0.008
Displaced by Another	0.5441 (0.329)	0.000	2.692	0.199

* $p < 0.05$

Table 6: Comparison of the average percentages (SE) of silverback behaviors observed in two group structures: multi-silverback mixed sex troops (n=4) and traditional family troops (n=2). Values are shown as the average of the gorillas' percentage of time spent exhibiting the behavior per visible hour. This table only includes interactions between the silverbacks and females or juveniles.

Behavior	**Mean Percent (SE)**		**F**	***P***
	Multi-Silverback	**Traditional Family**		
Aberrant	4.968 (2.407)	0.937 (0.930)	0.158	0.717
Receive Affiliation	0.9649 (0.551)	3.8853 (3.48974)	0.586	0.500
Initiate Affiliation	0.7607 (0.305)	1.7517 (1.68579)	0.064	0.817
Receive Aggression	0.1827 (0.091)	0.0625 (0.06250)	0.456	0.548
Initiate Aggression	0.2679 (0.069)	0.4080 (0.34204)	0.003	0.961
Displace Another	0.6818 (0.365)	0.3750 (0.375)	6.874	0.079
Displaced by Another	0.1075 (0.065)	0.000	8.178	0.064

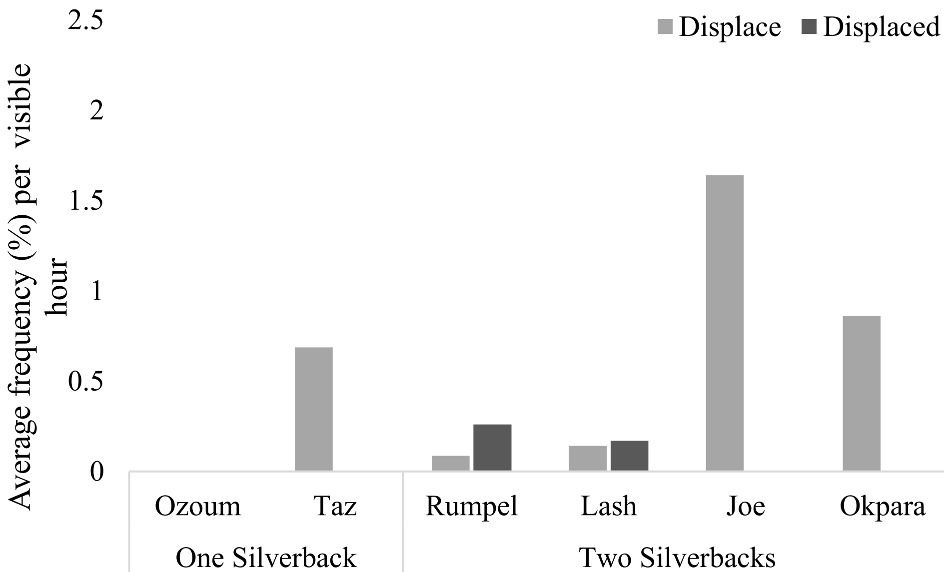


Figure 2: Average frequency per visible hour in which the six silverbacks engaged in submissive or dominant behavior by either displacing a conspecific female or being displaced by a conspecific female. Silverbacks were divided based on the type of social group they reside in. Rates of silverback displacements of each other have been removed for this graph.

Table 7: Calculated Z-scores for an index of asymmetry which illustrate the directionality of social behaviors for each silverback. Z-scores range between 1 and -1, where positive Z-scores indicate more silverback-initiated interactions. The magnitude of the Z-scores reveal the degree at which the silverback initiated interactions over the conspecific; Z-scores closer to 0 indicate more equal initiation from both individuals and scores closer to -1 or 1 reveal one-sided social interactions.

Group Composition	**Zoo**	**Silverback**	**Prosocial**	**Aggression**	**Displacements**
Multi-Silverback	JZG	Rumpel	-0.436	0.235	-0.478
		Lash	0	-0.385	-0.238
	FPZ	Joe	0.130	0.930	1
		Okie	0.5	0	1
Traditional Family	ZA	Ozoum	-0.714	1	1
		Taz	-0.354	0.714	1

Table 8: Percentage of scans gorillas spent touching, within 2 m, or further than 1 m from a conspecific.

		Mean Percent (SE)			
Gender	**Behavior**	**Multi-Silverback**	**Traditional Family**	**F**	***p***
Male	Contact	0.599 (0.599)	0.556 (0.556)	0.021	0.895
	Proximate	15.25 (7.81)	1.11 (1.11)	0.048	0.841
	Distant	84.15 (8.32)	98.333 (1.667)	0.169	0.687
Female	Contact	3.464 (2.461)	6.128 (5.238)	0.089	0.772
	Proximate	31.695 (6.635)	5.182 (1.121)	6.630	*.030
	Distant	64.841 (8.213)	88.61 (5.776)	3.623	0.089

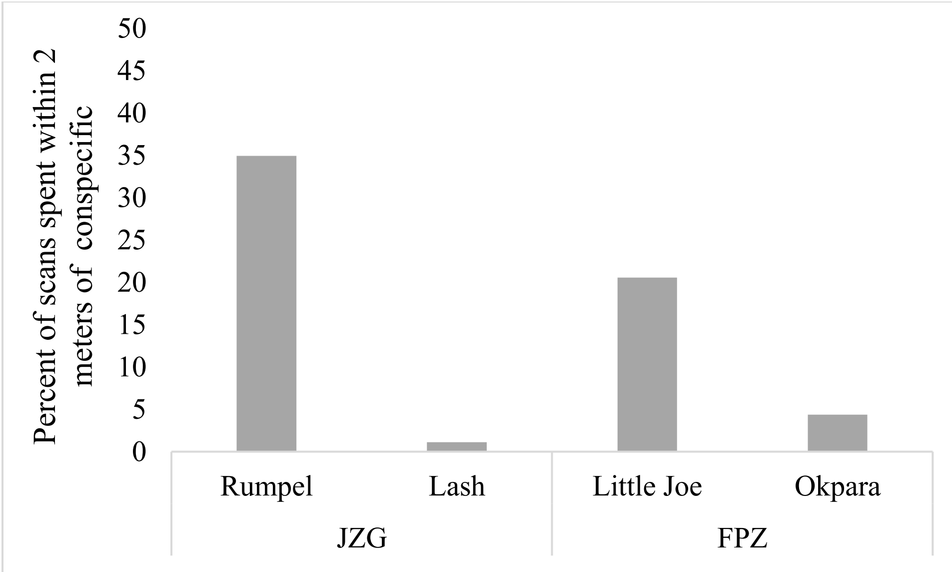
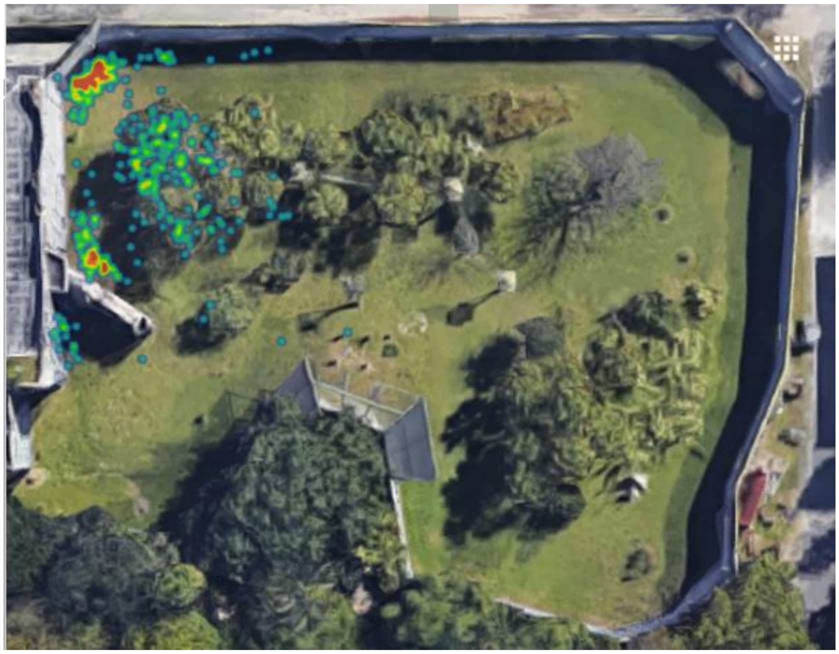


Figure 3: Percent of interval scans in which the four silverbacks housed in multi-male mixed-sex troops spent within 2 m of a conspecific (JZG=Jacksonville Zoo and Gardens, FPZ=Franklin Park Zoo).

Table 9: The SPI scores for gorillas in two multi-silverback mixed-sex groups. The score ranges from 0 to 1 with scores closer to 0 indicating total enclosure use, while those closer to 1 indicate minimal overall space use.

Zoo	Gorilla	Gender	PSI Score
JZG	Rumpel	Male	0.901
	Lash	Male	0.914
	Bulera	Female	0.576
	Madini	Female	0.664
	Kumbuka	Female	0.384
FPZ	Little Joe	Male	0.257
	Okie	Male	0.409
	Gigi	Female	0.663
	Kiki	Female	0.336
	Kimani	Female	0.392

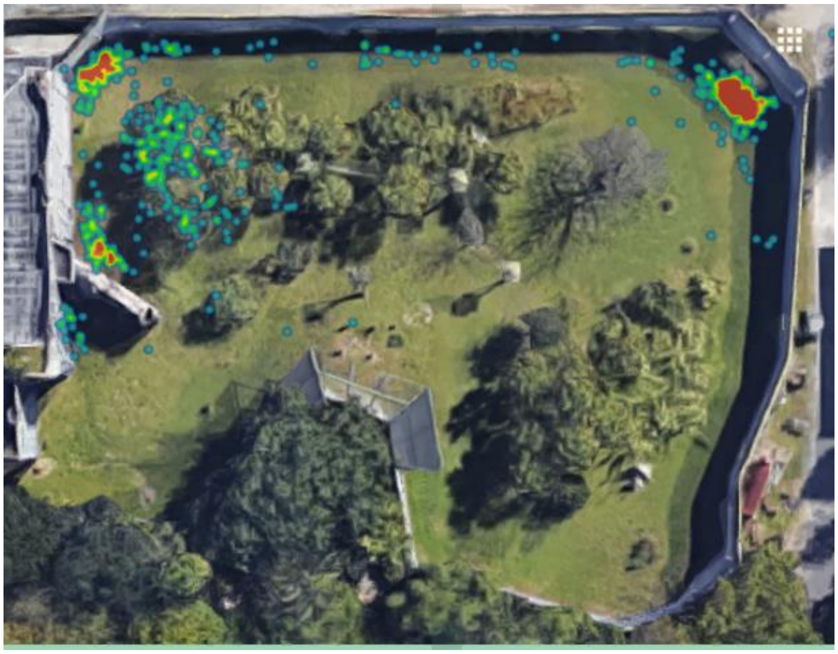
A.



B.

Figure 4: Space-use illustration of the two silverbacks in the multi-male mixed-sex troop at Jacksonville Zoo and Gardens. (A) Rumpel space-use (B) Lash space-use

A.



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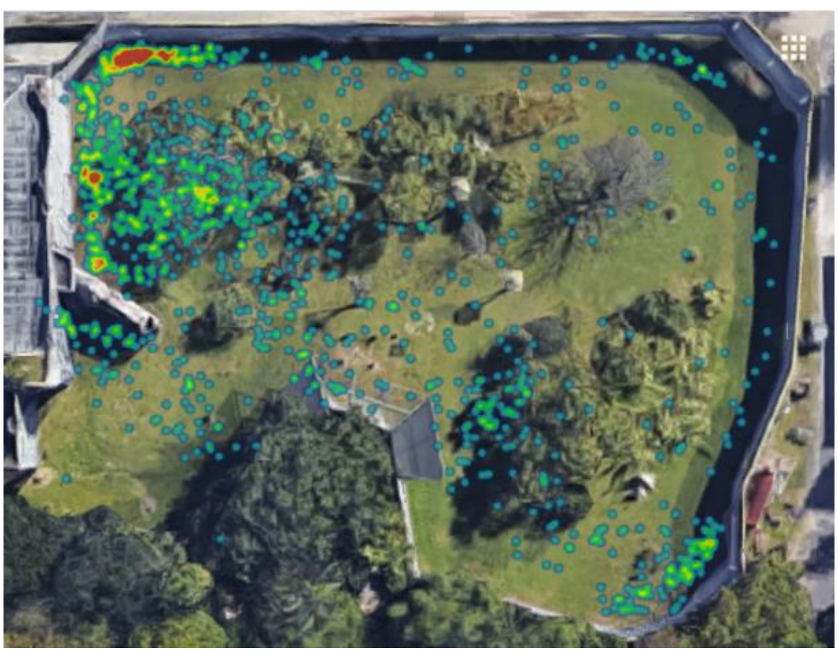
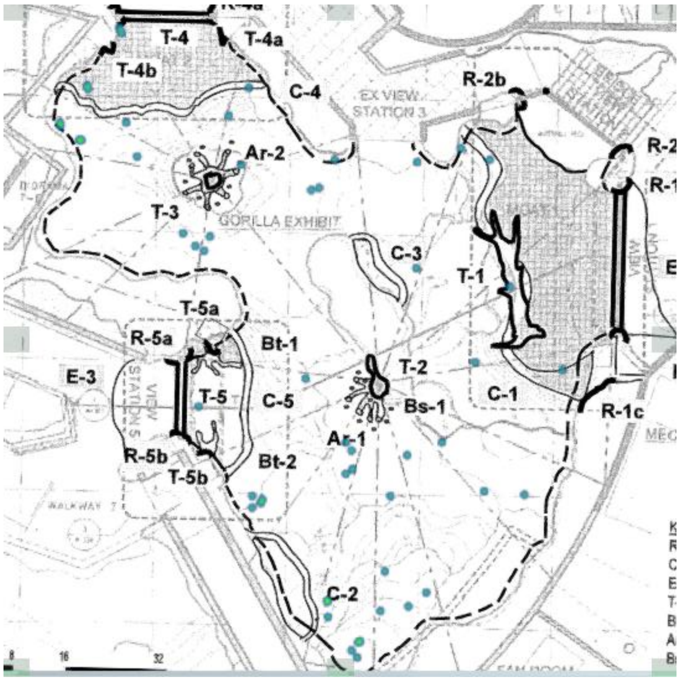


Figure 5: Space-use illustration of the five mature gorillas in the Jacksonville Zoo and Gardens troop. (A) Silverback [n=2] space-use (B) Female [n=3] space-use

A.



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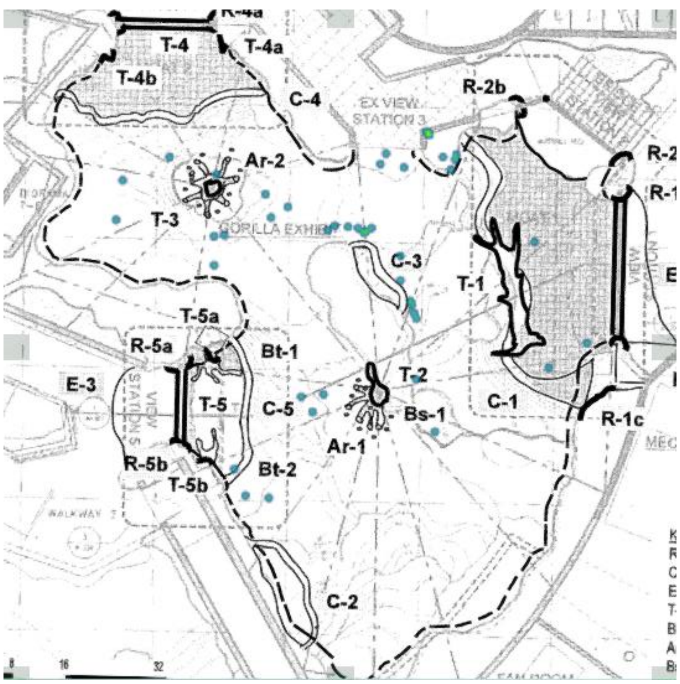
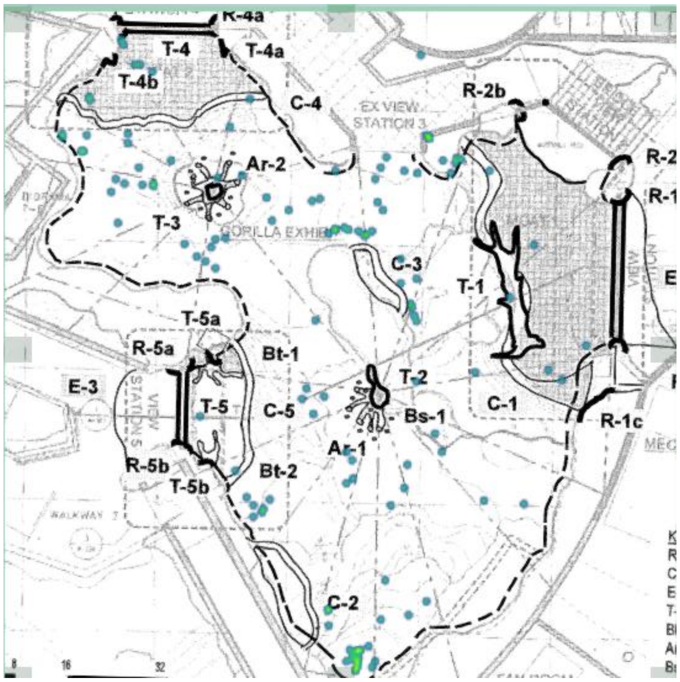


Figure 6: Space-use illustration of the two silverbacks in the multi-male mixed-sex troop at Franklin Park Zoo. (A) Little Joe space-use (B) Okpara space-use

A.



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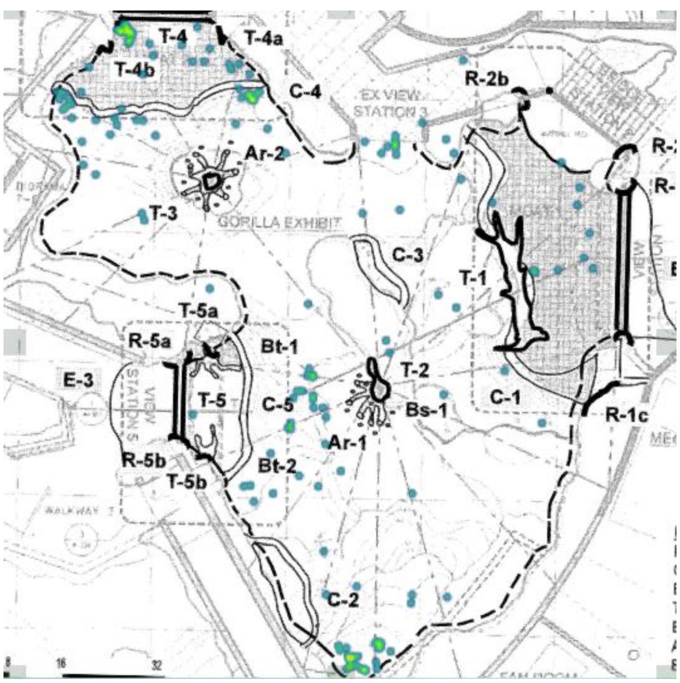


Figure 7: Space-use illustration of the five mature gorillas in the Franklin Park Zoo troop. (A) Silverback [n=2] space-use (B) Female [n=3] space-use

Table 10: Mean fecal glucocorticoid level (SD) for five mature gorillas housed at the Jacksonville Zoo and Gardens. As there were no low outliers, the last column reveals how many samples for each individual were high outliers, meaning their value was higher than two standard deviations above the gorilla's mean value.

Gorilla	Fecal Glucocorticoid Average (SD) ng/g	Number of Samples	Number of Outliers
Rumpel	256.304 (106.816)	41	1
Lash	632.033 (170.725)	42	2
Bulera	416.185 (223.059)	41	1
Madini	343.322 (165.855)	42	2
Kumbuka	247.523 (119.608)	42	2

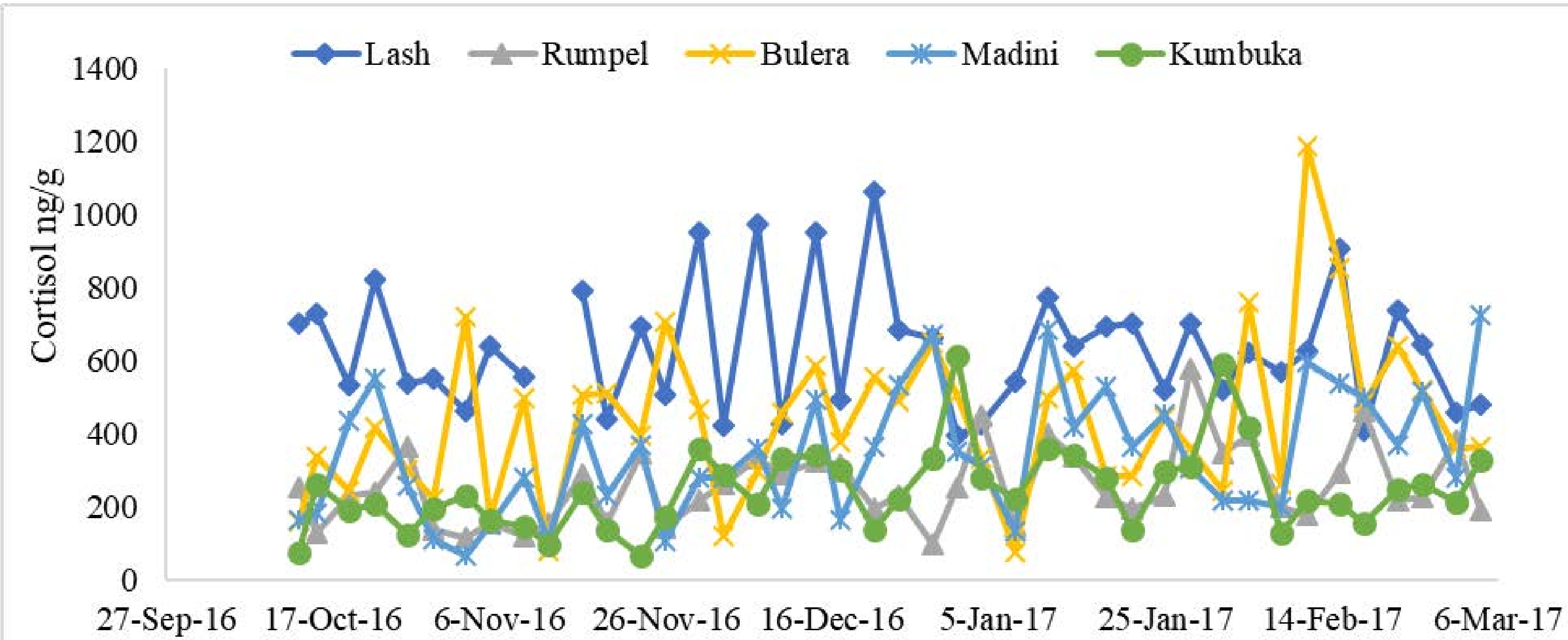
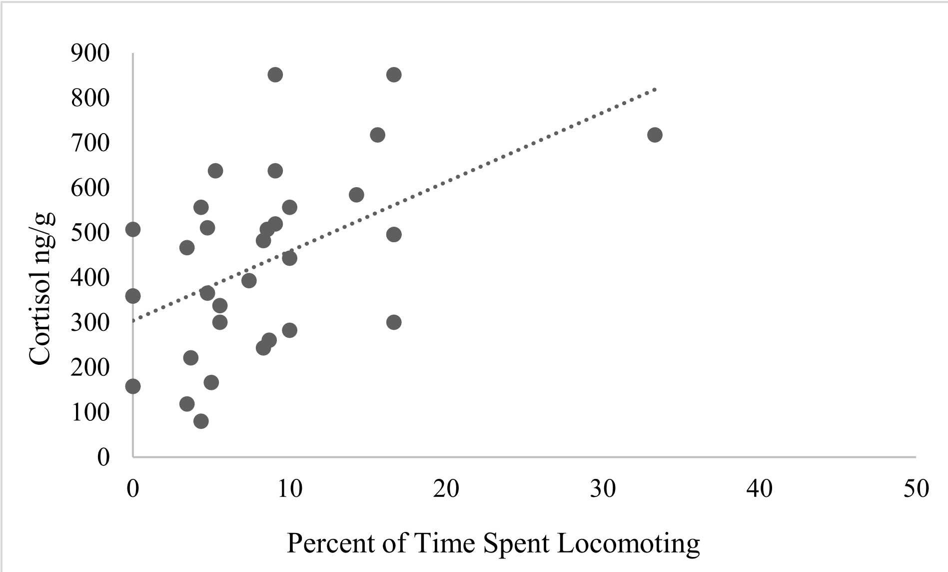


Figure 8: Overall fecal glucocorticoid (cortisol) levels for five gorillas housed at the Jacksonville Zoo and Gardens. Bulera's Jan 30th value was a known outlier which was excluded from analyses; however, it is included in this graphic.

Table 11: Binary logistic regression model including daily aggression occurrence and associated cortisol level for each gorilla housed at Jacksonville Zoo and Gardens.

				95% C.I. for EXP(B)	
	df	*p*	Exp(B)	Lower	Upper
Lash	1	0.659	0.999	0.995	1.003
Rumpel	1	0.431	0.997	0.991	1.004
Bulera	1	0.630	0.999	0.996	1.003
Madini	1	0.488	1.002	0.997	1.006
Kumbuka	1	0.887	1.000	0.994	1.006
Constant	1	0.693	1.964		

A.



B.

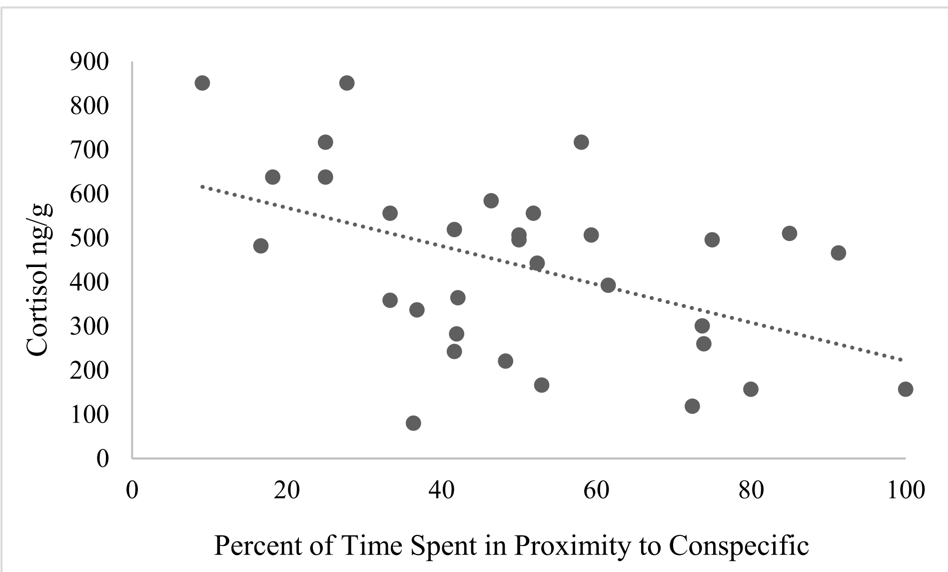


Figure 9: (A) The relationship between Bulera's fecal cortisol levels (ng/g) and observed frequency (%) of locomotion per day. (B) The relationship between Bulera's fecal cortisol levels (ng/g) and percent of time each observation day she spent in proximity to a conspecific. *Represented cortisol levels are expressed with a one to two-day lag time following observed behavior.

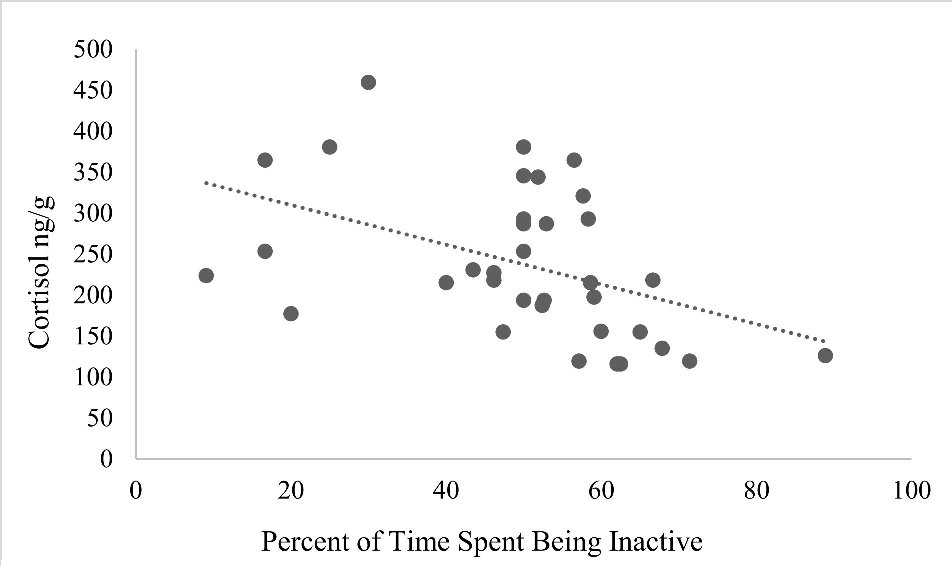


Figure 10: The relationship between Rumpel's fecal cortisol levels (ng/g) and observed frequency (%) of inactivity per day. *Represented cortisol levels are expressed with a one to two-day lag time following observed behavior.

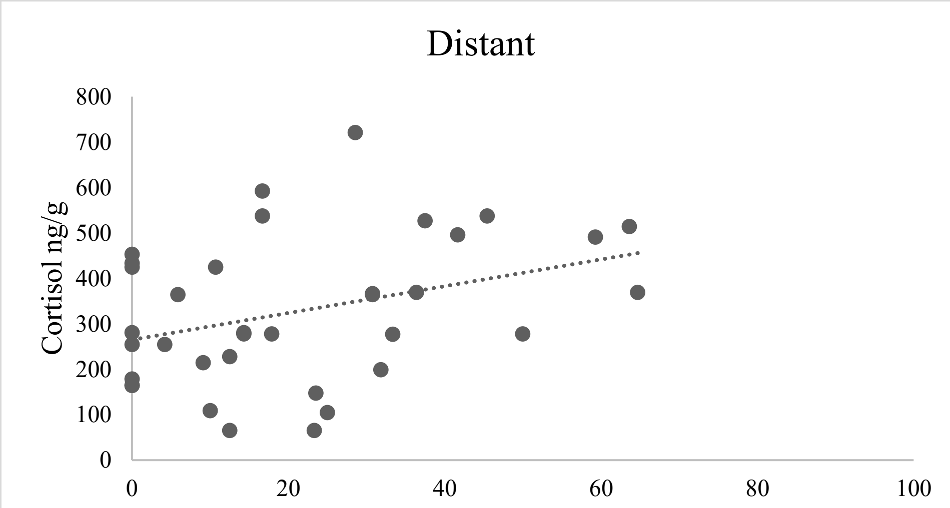


Figure 11: The relationship between Madini's fecal cortisol levels (ng/g) and the percent of time each observation day that she spent more than 2 m from a conspecific. *Represented cortisol levels are expressed with a one to two-day lag time following observed behavior.

Chapter 2

Multi-institutional survey on the recent history of multi-male heterosexual gorilla (*Gorilla gorilla gorilla*) troops outlining potential indicators of silverback compatibility in the North American SSP gorilla population

Abstract

Based on the growing population, it has been estimated that all North American zoological institutions housing gorillas (*Gorilla gorilla gorilla*) will need to separately house all-male groups, in addition to mixed-sex groups, within the next 50 years. The construction and implementation of these additional exhibits will require large amounts of human and monetary resources which will need to be planned for well in advance. Although it is commonly believed that male western gorillas do not tolerate one another in the presence of females, such social structure has, albeit rarely, been observed in the wild. As of 2016, only four of the 51 institutions housing gorillas in the North American Species Survival Plan® population housed multi-male mixed-sex groups. Some zoos have successfully managed such groups in the past, while others have tried and failed, leading to the ultimate transfer of one or all males. If the zoo community could determine how to successfully house more males together in breeding situations, it could open new opportunities for the gorilla population. This study encompassed a multi-institutional survey assessing whether ontogenetic or environmental characteristics could be associated with male compatibility in mixed-sex groups. Results suggest that successful multi-male mixed-sex groups were associated with males that were closely related, had been introduced at a younger age, and had been hand-reared at some time in their infancy. The goal of this study was to assess a potentially underutilized social grouping for zoo-housed gorillas and determine best management practices for gorillas in human care.

Introduction

Western lowland gorillas (*Gorilla gorilla gorilla*) are currently the only subspecies of gorilla housed in North American zoos. As of 2015, there were 353 western lowland gorillas, 168 males and 185 females, residing in these zoos, most of which were accredited by the Association of Zoos and Aquariums (Lukas et al., 2015). Based on recognized life history traits and ecology (Breuer et al., 2010; 2012; Stokes et al., 2003), zoos strive to house their gorillas in traditional family, or mixed-sex, groups with one silverback and multiple females (Leeds et al., 2015; Stoinski et al., 2001b; 2013). However, successful zoo breeding programs and a nearly 50:50 birth sex ratio has created the need to house surplus males in solitary conditions and, more commonly, in all-male groups, otherwise known as bachelor groups (Stoinski et al., 2013).

Although there are challenges associated with managing all-male groups in captivity (Coe et al., 2009; Stoinski et al., 2004b), such troops have been observed in the wild and, compared to solitude, are deemed more appropriate for gorilla welfare (Johnstone-Scott, 1988; Stoinski et al., 2002; 2004b). Based on the growing captive population, it has been estimated that all institutions housing gorillas will need to separately house all-male groups in addition to mixed-sex groups within the next 50 years (Stoinski et al., 2004b). The construction and implementation of these additional exhibits will require large amounts of human and monetary resources. To negate this issue, some zoos are attempting other housing possibilities. Although it is commonly believed that aggression will increase between male western lowland gorillas in the presence of females (Breuer et al., 2010; Robbins et al., 2004), family troops with multiple silverbacks have been observed in wild western lowland populations (Parnell, 2002; Robbins et al., 2004). For this reason, zoos have begun experimenting with this social. In 2016, four of the 51 institutions housing gorillas in the American Association of Zoos and Aquariums' (AZA)

Species Survival Plan® (SSP) population managed a mixed-sex group with more than one silverback (at least 14 yoa). Other institutions have tried and failed to house multiple silverbacks with females, resulting in the ultimate transfer of one or more males due to aggression. It has been suggested that multi-male mixed-sex groups may be more difficult to manage in zoo settings compared to bachelor groups for two reasons: the presence of females could result in higher levels of male aggression (Watts, 1990; Stoinski et al., 2004b) and zoo enclosures often provide fewer opportunities for males to avoid each other (Stoinski et al., 2004b). If the zoo community could determine how to successfully house more males together in breeding situations, it could revolutionize the future of gorilla management.

Currently, a Gorilla Behavior Advisory Group advises North American gorilla-housing institutions on how to facilitate tolerance within groups, but there have been no empirically denoted recommendations given to help encourage silverback amicability in mix-sexed environments. However, researchers have published some life history and environmental traits that may help relieve hostility between males in bachelor groups (Stoinski et al., 2004b; Coe et al., 2009). As part of an initiative to evaluate and improve the welfare of male gorillas in zoo settings, Stoinski and colleagues (2004b) outlined factors they believed were important to the successful formation of all-male groups. According to the authors' evaluations, age, and rearing history were some of the imperative variables. Specifically, they determined that the most stable groups were those in which members 1) were introduced before maturity, 2) were all parent reared or at least equally balanced between hand and parent reared, and 3) did not exceed four adult males.

As these previous studies have indicated, some variables, including individual life history traits and environmental characteristics, may impact the amiability of possible gorilla groups.

Thus, silverback compatibility could potentially be associated with such variables. To investigate this idea, an online survey was sent to institutions housing gorillas from North American Species Survival Program. The purpose of this survey was to assess whether certain ontogenetic or environmental characteristics may be associated with silverback compatibility.

Methods

The online survey was sent to the 51 gorilla-housing institutions via SurveyMonkey. This questionnaire was compiled of queries regarding the zoos' experiences within the past ten years dealing with multiple males in mixed-sex groups. For the sake of this study, such experiences included up to four scenarios: successfully introducing silverbacks (at least 14 yoa); attempting, and failing, to introduce silverbacks, leading to one's necessary transfer; successfully managing a group with an aging juvenile male (at least 11 yoa) and a silverback; and lastly, managing a group which led to the necessary transfer of an aging male juvenile due to growing aggression between him and the residing silverback. The survey focused on some of the factors previously determined to be important in the successful creation of gorilla bachelor groups (Stoinski et al., 2004b). Specifically, it included questions on relatedness of males, their rearing histories, the males' age difference at time of introduction, the number of females present at time of introduction, reproductive status of said females and whether infants or juveniles were present at time of introduction (Table 1). Though logistic regression would have been the preferential analysis given its ability to reveal predictors of male compatibility, a small sample size and complete separation of some factors rendered this type of assessment inappropriate. As an alternative, the survey responses were analyzed using a Multiple Correspondence Analysis (MCA) to outline potential associations between the management of successful multi-male mixed-sex groups and other surveyed factors. The MCA was conducted using Minitab 18 statistical software (MiniTab, 2017).

Results

There was a 92% survey completion rate; responses were received from 47 of the 51 institutions. Only one of the four missing institutions may have had relevant data for this study, as the other three have recent histories of managing either bachelor groups or solitary gorillas. Of the 47 participating institutions, only eleven had experience managing multi-male mixed-sex groups within the last 10 years. However, three of those eleven institutions had multiple experiences with separate multi-male scenarios. Therefore, there were fifteen multi-male mixed-sex groups and a total of 27 male gorillas analyzed for this study. Eleven of these fifteen scenarios represented successful multi-male groups while four of them described unsuccessful attempts of such groups.

For applications of the MCA, the survey responses were divided into 12 variables each with up to three mutually exclusive factors (Table 1). The principal inertia values portray proportions of the total inertia for the MCA model (Table 2). Each component's value represents the amount of variation accounted for by that dimension. These values are commonly used to determine the number of components that should be retained for the model. For this study, 'the average rule' was implemented (Wilson and Cooper, 2008). This rule states that those components which explain more than the average inertia of the total model should be kept. Using this guideline and the inertia values for each axis, the first six components were specified. These six axes accounted for 87.20 percent of the variation that could be explained by the twelve total variables (Table 2). Though these six components were used for the modeling, interpreting all six was not needed. Similar to principal component analyses, the model sequentially lists the components based on the amount of variance explained. Meaning, the first component explains as much variance as possible, and the second component listed explains as much of the remaining variance as possible and so on. For this reason, only up to three components are generally interpreted in multidimensional scaling (Ayele et al., 2014). Thus, the first two components of the Euclidean space were plotted to determine potential relationships between successful multi-male groups and the other outlined ontogenetic and environmental factors.

Interpretation of MCA graphs revolves around the placement of each factor's point within a plot. Those points which are in the approximate same direction and region of space are those which show association. Therefore, this MCA illustrates that successful multi-male groups were most closely associated with rearing history, relatedness, and whether the males in question have ever been managed in a bachelor group (Figure 1). Specifically, the results indicate that successful multi-male mixed-sex groups were more frequent when both males had been hand-reared, males were either father and son or siblings, and neither male had ever been housed in a bachelor group (Figure 1). The MCA also illustrated an association between successful multi-male heterosexual groups and males who had both had past experiences with a silverback, males that were introduced when they were both infants or juveniles, and males that had never been housed in solitary conditions. Conversely, unsuccessful multi-male groups were associated with less related males, males that had been parent reared, males that had ever been managed in either bachelor or solitary conditions, and males that had not had any previous experiences with a silverback prior to their introduction (Figure 1). There seemed to be little to no association between group success and the number of infants and females present or whether said females were reproductively active. Similar patterns of association between these variables are illustrated in the plots for components three through six (Figure 2).

Discussion

The survey for this analysis was largely structured off the former publication by Stoinski and associates (2004b) which outlined factors to consider when attempting to form successful gorilla bachelor groups in a zoo setting. Although their paper strictly dealt with the formation of bachelor groups, it is highly plausible that the consideration of the same factors may be beneficial in the implementation of multi-male mixed-sex groups, and there was certainly overlap between their conclusions and the present findings.

In accordance with the beliefs of Stoinski et al., the current study found that male relatedness was associated with the success of multi-male groups. Stoinski et al., suggested that relatedness, or at least familiarity, could be involved in the maintenance of positive relationships between males in bachelor groups. This notion is supported by an additional study conducted by Stoinski et al (2004a), which explored the social dynamics and relationships between zoo-managed bachelor groups. In one bachelor group consisting of a silverback, his juvenile son and two unrelated juveniles, higher rates of affiliative interactions were observed between the silverback and his son compared to the silverback and the unrelated juvenile. Additionally, the majority of wild mountain gorilla multi-male troops are composed of related males (Robbins, 2001). Robbins' 1996 study on mountain gorilla male dyads even suggested that maternal relatedness may be a necessary factor in in the development of long-lasting relationships between males in mixed-sex groups. Thus, it could be that these wild multi-male groups are formed around the basis of the familiarity of related individuals (Harcourt & Stewart, 1981).

This analysis also supported the suggested made by Stoinski et al. (2004b), that age may play an important role in the formation and maintenance of male groups. The MCA determined that successful multi-male groups were associated with males that had been introduced as infants or juveniles. This is similar to findings that bachelor groups formed with immature males are more successful than those formed with adult males (Porton & White, 1996; Stoinski et al., 2008). Even in the wild, most all-male groups are formed when juvenile males disperse from their natal group (Robbins, 1995). There are very few documented cases of silverbacks joining all-male groups (Yamagiwa, 1987). Moreover, only one zoo from the current study managed a successful multi-male heterosexual group in which the males had been introduced as silverbacks. All other successes involved males introduced as juveniles or infants or introductions between a silverback and an infant or juvenile. In addition, age has been determined to be the best predictor in male gorilla behavior (Stoinski et al., 2013). Specifically, higher rates of affiliative and lower rates of aggressive interactions have been shown to be associated with younger ages in male gorillas (Stoinski et al., 2004a; Stoinski et al., 2013). Thus, the present results mirror the suggestion of Stoinski and colleagues; it seems that introduction between males in any group type may be more successful when they are done at a younger age during which affiliative interactions are more likely to occur, hence lending more time and a more positive environment to develop affiliative relationships. However, it should be noted that the teenage years in male gorillas, 14-20 yoa, have been shown to be correlated with high levels of non-contact aggression and peaking testosterone levels (Stoinski et al., 2002; 2004a; 2013). Thus, it may be more beneficial to plan on introductions before a male reaches that period. Even so, one of the four zoos housing multi-male mixed-sex groups in 2016 successfully managed a group whose two silverbacks were both in this age range.

Interestingly, the current assessment provided some results that were at odds with the suggestion made by Stoinski and colleagues (2004b). The MCA revealed that successful multi-male groups were associated with hand-reared males. Though it was once considered commonplace, the unnecessary hand-rearing of primates is now usually regarded with contempt in zoo-settings as it has been linked to the expression of aberrant or species-atypical behaviors and inappropriate conspecific interactions (Maple, 1980; Meder, 1989, Fritz et al., 1992; Marriner & Drickemer; 1994; Ryan et al., 2002; Porton & Niebruegge, 2006; Jacobson et al., 2016). Today, hand-rearing in accredited zoos is generally only done as a last resort, when the mother cannot or will not take care of the infant herself and no surrogate mother is available (Porton & Niebruegge, 2006). Stoinski and colleagues noted that hand-rearing may compromise individual success in all-male groups (2004b). It was even determined that hand-reared males had a higher tendency to be removed from bachelor groups due to growing aggressive interactions between them and other troop members (Stoinski et al., 2004a). Hand-reared primates have also been shown to exhibit lower levels of affiliative interactions with conspecifics (Meder, 1989; Jacobson et al., 2016). Moreover, bachelor groups comprised solely of hand-reared males were determined to have affiliative interaction rates that were 30 times lower than those of bachelor groups a mixture of hand and parent-reared males (Stoinski et al., 2004a).

Thus, the association between the success of multi-male mixed-sex groups and hand-reared males may be an artifact of a higher proportion of hand-reared males in the present study. Between 1970 and 1996, the annual proportional frequencies of hand rearing occurrences for North American zoo-housed western lowland gorillas ranged from 27% to 67% of the total population (Ryan et al., 2002). As the majority (n=22) of males in the current assessment were born during that period, it’s understandable that at least one silverback in 12 of the 15 groups analyzed for this study was hand-reared at some point in infancy. This biasing could have over-inflated the association. Even so, it could be possible that unique factors to the multi-sex groups in relation to bachelor groups, including the presence of females, could be improving the success of hand-reared males in these settings. The author in no way suggests that more male gorillas should be hand-reared to improve their likelihood of successful introduction into a multi-male mixed-sex groups; however, if the implementation of more multi-male groups becomes likely, it may be advantageous to start with males that have been hand-reared.

Another unexpected finding was that success was associated with males that had never been housed in a bachelor group or in solitary conditions. Bachelor groups and even solitary males are observed in the wild and are considered natural social structures (Yamagiwa, 1987; Robbins, 1996; 2001; Parnell, 2002; Watts, 2002); however, they are thought to be transitory, as bachelor groups will usually disband, and solitary males will find females, when they become sexually mature (Robbins, 1996; Watts, 2002). Given this, it would seem likely that such social structures could be used as transitional groups for male gorillas in zoo settings. However, a study on the physiology of male gorillas determined that solitary males had significantly higher levels of cortisol compared to males of their same age that were housed in social settings. Thus, this indicates that solitude may not be an adequate condition for zoo-housed gorillas. Furthermore, given that males kept in solitude would not have had experience with other male gorillas, it would make sense that they may not know how to appropriately interact with them, especially around females. This postulation is supported by the finding that success in this analysis was also associated with male pairs that had both had previous experience with a silverback(s).

Aside from the challenges often associated with their management (Stoinski et al., 2013), zoo bachelor groups have proved highly successful (Stoinski et al., 2002; 2004a). There have been several successful male transitions from such bachelor groups into mixed-sex breeding situations (Stoinski et al., 2013). Thus, theorizing why multi-male groups were more successful when the males had never been managed in a bachelor groups is more difficult. It could be that males from bachelor groups are used to interacting with other males by themselves, but do not know how to do so in the presence of females. It could also be that in the current study, those males who had previous experience in a bachelor group may have been introduced into the bachelor group at a young age and thus did not have much exposure to or experience with a silverback around females.

Although these findings suggest there was an association between successful multi-male groups and several ontogenetic factors, it is important to note that such factors are not necessarily a prerequisite for, or would they guarantee future success. However, this study does offer a starting point for the consideration of male candidates for potential multi-male groups. Thoughtful management strategies are still needed for the surplus males in the gorilla population (Stoinski et al., 2013). The 50:50 birth-sex ratio ensures there will always be a need for bachelor groups; however, institutions may not need as many bachelor groups as was once estimated. The results from this study indicate multi-male mixed sex groups may be another viable option for surplus males. Potentially, bachelor and multi-male groups could be managed in a way that benefits gorillas in both group settings. For instance, there are some males in the population who will likely never breed due the over-representation of their genetics in the population (Lukas et al., 2015). Thus, a potential strategy would be to continue to house those males in bachelor groups, while transitioning the potential breeding males from their natal groups into multi-male mixed-sex groups. The continued experience with females may prove beneficial for their reproductive success. Additionally, as parent-reared or an equal mix of parent and hand-reared males seem to be better suited for bachelor groups (Stoinski et al., 2004a; 2004b), perhaps parent-reared males could be transitioned into bachelor groups while more hand-reared males are retained in mixed-sex groups. Of course, all groups would need to be closely monitored as multi-male group dynamics can differ between individual groups (Chapter 1).

Acknowledgements

An immense thank you goes to the Chair of the Gorilla Species Survival Plan®, Dr. Kristen Lukas, for dispersing the surveys to the 51 SSP gorilla institutions. My additional gratitude goes to each director, curator, and keeper who took the time out of their busy schedule to complete the survey. Without their input, this work would not have been possible.

Table 1: Survey response variables assessed in the Multiple Correspondence Analysis. The variable abbreviation indicated in the MCA plot are included in parenthesis when applicable.

Variable (plot abbreviation)	**Factor**	**Definition**
Success	Yes	A multi-male group had been successfully managed.
	No	An attempt to manage a multi-male was made, but it was unsuccessful, and led to the transfer of one of the males.
Rearing (rear)	Hand	All males in question were reared by humans at some point in infancy.
	Parent	All males in question were reared by a biological or surrogate gorilla mother throughout infancy.
	Mix	At least one male in question was reared by humans at some point in infancy.
Silverback Experience (exp)	Both	All males in question were raised with a silverback or had experience with a silverback before introductions occurred.
	Neither	None of the males in question were raised with a silverback or had experience with any silverback before introductions occurred.
	Mix	At least one of the males in question had no experience with any silverback prior to introduction.
Solitary	Yes	At least one male in question had been previously housed in solitary conditions.
	No	None of the males in question had ever been housed in solitary conditions.
Bachelor	Yes	At least one male in question had been previously housed in a bachelor group.
	No	None of the males in question had ever been housed in a bachelor group.
Number of females (female)	0	No females were present at the time of introduction.
	1	One to two females were present at the time of introduction.
	2	More than two females were present at the time of introduction.
Female reproductive status (fem_repro)	Yes	At least one female present at the time of introduction was reproductively active.
	No	No present females were reproductively active.

Infant	Yes	At least one infant was present at the time of introduction.
	No	No infants were present at the time of introduction.
Relation (relate)	0	The males in questions were not closely related.
	1	The males in question were first cousins.
	2	The males in question were either half-siblings, grandfather/grandson, or uncle/nephew.
	3	The males in question were either full siblings or father/son.
Age group	Two silverbacks	All males in questions were at least 14 yoa at the time introduction.
	Silverback and juvenile	At least one male in question was less than 14 yoa and one was over 14 yoa at the time introduction (includes infants born and maintained in group with silverback).
	Two juveniles	All males in questions were under 14 yoa at the time introduction.

Table 2: Analysis of indicator matrix for Multiple Correspondence Analysis.

Axis	Inertia	Proportion	Cumulative	Histogram for accounted variance in model
1	0.3412	0.2409	0.2409	******************************
2	0.2429	0.1714	0.4123	*********************
3	0.1955	0.1380	0.5503	*****************
4	0.1823	0.1287	0.6790	****************
5	0.1469	0.1037	0.7827	************
6	0.1265	0.0893	0.8720	***********
7	0.0655	0.0462	0.9182	*****
8	0.0450	0.0317	0.9500	***
9	0.0382	0.0269	0.9769	***
10	0.0215	0.0152	0.9921	*
11	0.0095	0.0067	0.9988	
12	0.0017	0.0012	1.0000	
Total	1.4167			

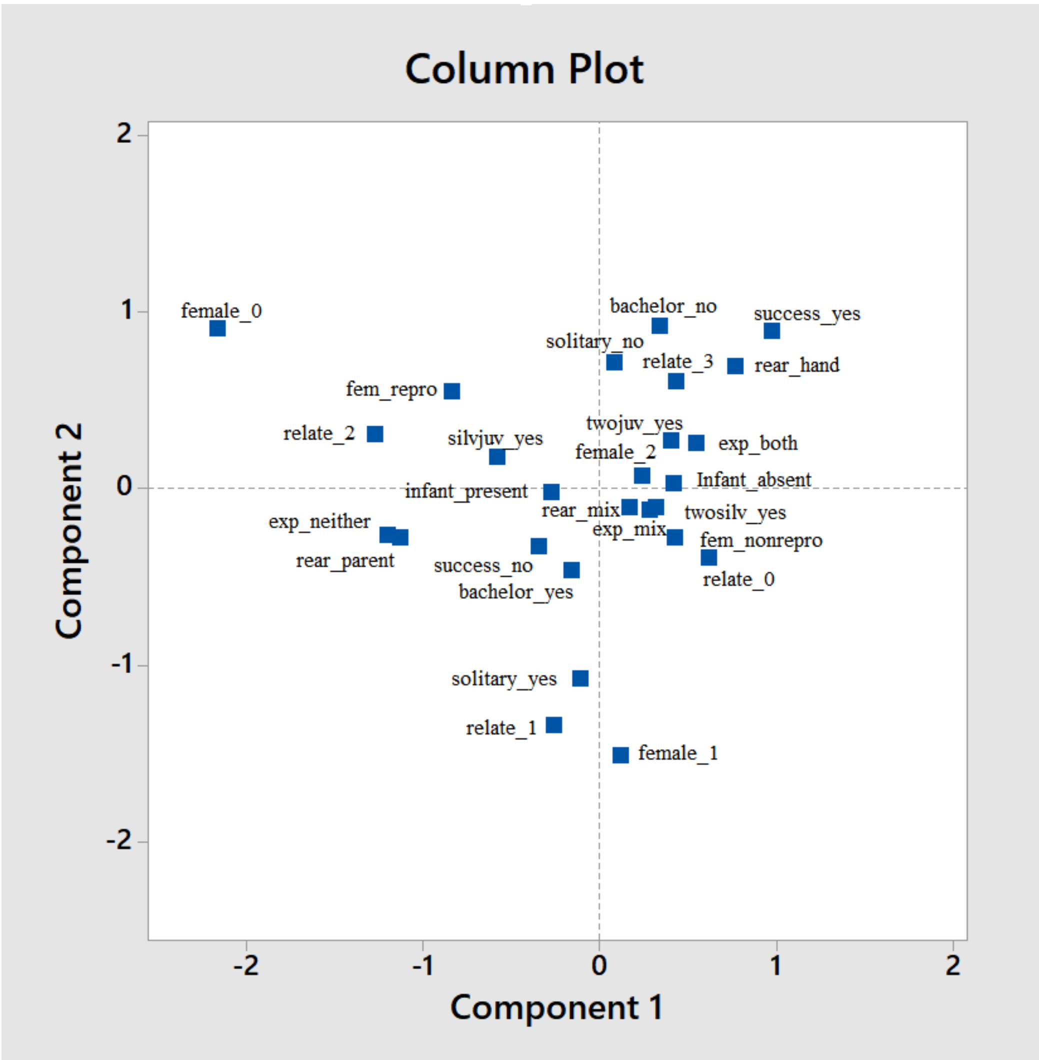


Figure 1: Multiple correspondence analysis plot for components one and two which explains 41% of the total variance explained by the model. The graphic illustrates associations between the success of multi-male troops (success_yes) and other ontogenetic factors of the silverbacks in questions.

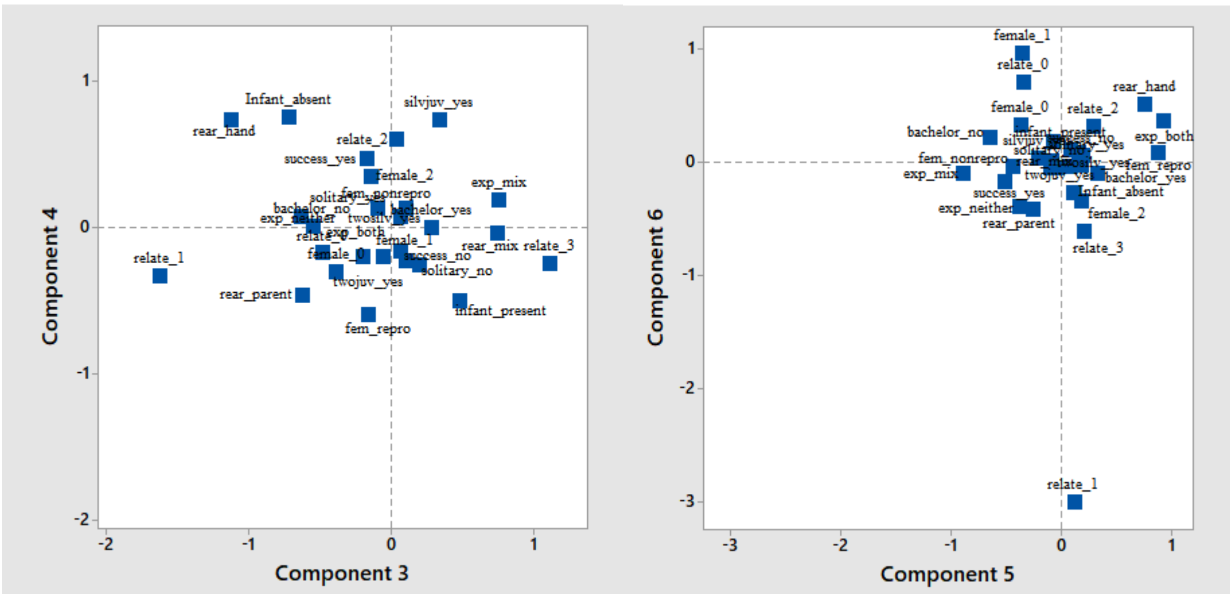


Figure 2: Multiple correspondence analysis plot for components three through six.

Bibliography

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227-266.

Aureli, F., & De Waal, F. (1997). Inhibition of social behavior in chimpanzees under high-density conditions. *American Journal of Primatology*, *41*(3), 213-228.

Ayele, D., Zewotir, T., & Mwambi, H. (2014). Multiple correspondence analysis as a tool for analysis of large health surveys in African settings. *African health sciences*, *14*(4), 1036-1045.

Bahr, N.I., Palme, R., Mohle, U., Hodges, J.K. & Heistermann, M. (2000) Comparative aspects of the metabolism and excretion of cortisol in three individual nonhuman primates. *General and Comparative Endocrinology*, 117, 427-438.

Bettinger, T., Kuhar, C., Sironen, A., Goldstein, M., & Laudenslager, M. L. (2001). Behavior and salivary cortisol in an all-male gorilla group. *American Journal of Primatology*, 49, 35.

Boinski, S., Swing, S. P., Gross, T. S., & Davis, J. K. (1999). Environmental enrichment of brown capuchins (Cebus apella): behavioral and plasma and fecal cortisol measures of effectiveness. *American Journal of Primatology*, 48(1), 49-68.

Bonnie, K. E., Ang, M. Y., & Ross, S. R. (2016). Effects of crowd size on exhibit use by and behavior of chimpanzees (Pan troglodytes) and Western lowland gorillas (Gorilla gorilla) at a zoo. *Applied Animal Behaviour Science*, *178*, 102-110.

Bradley, B. J., Robbins, M. M., Williamson, E. A., Steklis, H. D., Steklis, N. G., Eckhardt, N., ... & Vigilant, L. (2005). Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups. *Proceedings of the National Academy of Sciences of the United States of America*, 102(26), 9418-9423.

Breuer, T., Robbins, A. M., Olejniczak, C., Parnell, R. J., Stokes, E. J., & Robbins, M. M. (2010). Variance in the male reproductive success of western gorillas: acquiring females is just the beginning. *Behavioral Ecology and Sociobiology*, *64*(4), 515-528.

Broom, D., & Johnson, K. G. (1993). Approaching questions of stress and welfare. *Stress and Animal Welfare*, 1-7.

Burks, K. D., Bloomsmith, M. A., Forthman, D. L., & Maple, T. L. (2001). Managing the socialization of an adult male gorilla (Gorilla gorilla gorilla) with a history of social deprivation. *Zoo Biology*, *20*(5), 347-358.

Caillaud, D., Levréro, F., Gatti, S., Menard, N., & Raymond, M. (2008). Influence of male morphology on male mating status and behavior during interunit encounters in western lowland gorillas. *American Journal of Physical Anthropology*, *135*(4), 379-388.

Cavigelli, S. A. (1999). Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, Lemur catta. *Animal Behaviour*, 57(4), 935-944.

Clark, F. E., Fitzpatrick, M., Hartley, A., King, A. J., Lee, T., Routh, A., Walker S, & George, K. (2012). Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology*, *31*(3), 306-321.

Coe, C. L., & Levine, S. (1995). Diurnal and annual variation of adrenocortical activity in the squirrel monkey. *American Journal of Primatology*, *35*(4), 283-292.

Coe, J. C., Scott, D., & Lukas, K. E. (2009). Facility design for bachelor gorilla groups. *Zoo Biology, 28*(2), 144-162.

Crockett, C. M., & Ha, R. R. (2010). Data collection in the zoo setting, emphasizing behavior. *Wild Mammals in Captivity: Principles and Techniques for Zoo Management. The University Of Chicago Press, Chicago*, 386-406.

Dickens, M. (1955). A statistical formula to quantify the "spread-of-participation" in group discussion. *Speech Monographs*, 22, 28-31.

Doran, D. M. (2001). Subspecific variation in gorilla behavior: the influence of ecological and social factors. Mountain gorillas: Three decades of research at Karisoke, 123-149.

Eckardt, W., Fawcett, K., & Fletcher, A. W. (2016). Weaned age variation in the Virunga mountain gorillas (*Gorilla beringei beringei*): influential factors. *Behavioral ecology and sociobiology*, *70*(4), 493-507.

Fossey, D. (1983). Gorillas in the mist. Boston, MA: Houghton Mifflin.

Fritz, J., Nash, L.T., Alford, P.L., Bowen, J.A. (1992). Abnormal behaviors, with a special focus on rocking, and reproductive competence in a large sample of captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology 27*(3):161-176

Fuller, G., Margulis, S. W., & Santymire, R. (2011). The effectiveness of indigestible markers for identifying individual animal feces and their prevalence of use in North American zoos. *Zoo Biology*, *30*(4), 379-398.

Gatti, S., Levréro, F., Ménard, N., Petit, E., & Gautier-Hion, A. (2003). Bachelor groups of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoue Clearing, Odzala National Park, Republic of Congo. *Folia Primatologica*, *74*, 195-196.

Gatti, S., Levréro, F., Ménard, N., & Gautier-Hion, A. (2004). Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoue, Republic of Congo. *American Journal of Primatology*, 63(3), 111-123.

Girard, I., & Garland, T. (2002). Plasma corticosterone response to acute and chronic voluntary exercise in female house mice. *Journal of applied physiology*, *92*(4), 1553-1561.

Gray, M., McNeilage, A., Fawcett, K., Robbins, M. M., Ssebide, B., Mbula, D., & Uwingeli, P. (2010). Censusing the mountain gorillas in the Virunga Volcanoes: complete sweep method versus monitoring. *African Journal of Ecology, 48*(3), 588-599.

Greco, B. J., Meehan, C. L., Hogan, J. N., Leighty, K. A., Mellen, J., Mason, G. J., & Mench, J. A. (2016). The days and nights of zoo elephants: using epidemiology to better understand stereotypic behavior of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. *PLoS One*, *11*(7), e0144276.

Harcourt, A.H., & Stewart, K.J. (1981). Gorilla male relationships: can differences during immaturity lead to contrasting reproductive tactics in adulthood? *Animal Behavior* 29:206–10.

Harcourt, A. H., & Stewart, K. J. (2007). Gorilla society: What we know and don't know. *Evolutionary Anthropology: Issues, News, and Reviews*, *16*(4), 147-158.

Heistermann, M., Palme, R., & Ganswindt, A. (2006). Comparison of different enzymeimmunoassays for assessment of adrenocortical activity in primates based on fecal analysis. *American Journal of Primatology*, *68*(3), 257-273.

Hoff, M. P., Hoff, K. T., & Maple, T. L. (1998). Behavioural response of a Western lowland gorilla (*Gorilla gorilla gorilla*) group to the loss of the silverback male at Zoo Atlanta. *International zoo yearbook*, *36*(1), 90-96.

Hoff, M. P., Hoff, K. T., Horton, L. C., & Maple, T. L. (1996). Behavioral effects of changing group membership among captive lowland gorillas. *Zoo Biology*, *15*(4), 383-393.

Hoff, M. P., Nadler, R. D., & Maple, T. L. (1982). Control role of an adult male in a captive group of lowland gorillas. *Folia Primatologica*, *38*(1-2), 72-85.

Hoff, M. P., Powell, D. M., Lukas, K. E., & Maple, T. L. (1997). Individual and social behavior of lowland gorillas in outdoor exhibits compared with indoor holding areas. *Applied Animal Behaviour Science*, *54*(4), 359-370.

IBM Corp. Released 2016. IBM SPSS Statistics for Windows, Version 24.0. Armonk, NY: IBM Corp.

Jacobson, S. L., Ross, S. R., & Bloomsmith, M. A. (2016). Characterizing abnormal behavior in a large population of zoo-housed chimpanzees: prevalence and potential influencing factors. *PeerJ*, *4*, e2225.

Johnstone-Scott, R. A. (1988). The potential for establishing bachelor groups of western lowland gorillas (*Gorilla gorilla gorilla*). Dodo, 25, 61-66.

Kalpers, J., Williamson, E. A., Robbins, M. M., McNeilage, A., Nzamurambaho, A., Lola, N., & Mugiri, G. (2003). Gorillas in the crossfire: population dynamics of the Virunga mountain gorillas over the past three decades. *Oryx*, *37*(3), 326-337.

Kenny, D. E., Cambre, R. C., Alvarado, T. P., Prowten, A. W., Allchurch, A. F., Marks, S. K., & Zuba, J. R. (1994). Aortic dissection: an important cardiovascular disease in captive gorillas (*Gorilla gorilla gorilla*). *Journal of Zoo and Wildlife Medicine*, 561-568.

Klailova M (2011). Interunit, Environmental and Interspecific Influences on Silverback-Group Dynamics in Western Lowland Gorillas (*Gorilla gorilla gorilla*). PhD dissertation, University of Stirling.

Krynak, K. L., Burke, D. J., Martin, R. A., & Dennis, P. M. (2017). Gut microbiome composition is associated with cardiac disease in zoo-housed western lowland gorillas (Gorilla gorilla gorilla). *FEMS Microbiology Letters*, *364*(15).

Kuhar, C. W., Bettinger, T. L., & Laudenslager, M. L. (2005). Salivary cortisol and behaviour in an all-male group of western lowland gorillas (*Gorilla gorilla gorilla*). *Animal Welfare*, *14*(3), 187-193.

Leeds, A., Boyer, D., Ross, S. R., & Lukas, K. E. (2015). The effects of group type and young silverbacks on wounding rates in western lowland gorilla (Gorilla gorilla gorilla) groups in North American zoos. *Zoo Biology*,*34*(4), 296-304.

Less, E.H., Lukas, K. E., Kuhar, C. W., & Stoinski, T. S. (2010). Behavioral response of captive western lowland gorillas (Gorilla gorilla gorilla) to the death of silverbacks in multi-male groups. *Zoo Biology*, *29*(1), 16-29.

Levrero, F. (2005). Structure d'une population de gorilles (*Gorilla gorilla gorilla*) visitant une clairière forestière: nature et rôle des rencontres intergroupes dans sa dynamique (Doctoral dissertation, Rennes 1).

Lukas, K. E. (1999). A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (Gorilla gorilla gorilla). *Applied Animal Behaviour Science*, *63*(3), 237-249.

Lukas, K. E., Elsner, E., Long, S., & Groome, C. (2015). Population analysis and breeding plan: Western lowland gorilla (*Gorilla gorilla gorilla*). Silver Spring, MD: Association of Zoos and Aquariums.

Lukas, K. E., Hoff, M. P., & Maple, T. L. (2003). Gorilla behavior in response to systematic alternation between zoo enclosures. *Applied Animal Behaviour Science*, *81*(4), 367-386.

Lukas, K. E., Kuhar, C. W., & Stoinski, T. S. (2010). Behavioral response of captive western lowland gorillas (Gorilla gorilla gorilla) to the death of silverbacks in multi-male groups. *Zoo Biology*, *29*(1), 16-29.

Lupien, S. J., de Leon, M., De Santi, S., Convit, A., Tarshish, C., Nair, N. P. V., Thakur M., McEwen B.S., Hauger R.L, & Meaney, M. J. (1998). Cortisol levels during human aging predict hippocampal atrophy and memory deficits. *Nature neuroscience*, *1*(1), 69-73.

Maestripieri, D., Ross, S. K., & Megna, N. L. (2002). Mother-infant interactions in western lowland gorillas (*Gorilla gorilla gorilla*): Spatial relationships, communication and opportunities for social learning. *Journal of Comparative Psychology*, *116*(3), 219.

Magliocca, F., & Gautier-Hion, A. (2002). Mineral content as a basis for food selection by western lowland gorillas in a forest clearing. *American Journal of Primatology*, *57*(2), 67-77.

Magliocca, F., Querouil, S., & Gautier-Hion, A. (1999). Population structure and group composition of western lowland gorillas in North-Western Republic of Congos. *American Journal of Primatology, 48*(1), 1-14.

Maple, T.L. (1980). Breaking the hand-rearing syndrome in captive apes. In: AAZPA Annual Conference Proceedings. American Association of Zoological Parks and Aquariums, Wheeling, WV.

Maple, T. L., & Finlay, T. W. (1986). Evaluating the environments of captive nonhuman primates. In Primates (pp. 479-488). Springer, New York, NY.

Margulis, S. W., Whitham, J. C., & Ogorzalek, K. (2003). Silverback male presence and group stability in gorillas (*Gorilla gorilla gorilla*). *Folia Primatologica*, *74*(2), 92-96.

Marriner, L. M., & Drickamer, L. C. (1994). Factors influencing stereotyped behavior of primates in a zoo. *Zoo Biology, 13*(3), 267-275.

Masi, S., Cipolletta, C., & Robbins, M. M. (2009). Western lowland gorillas (Gorilla gorilla gorilla) change their activity patterns in response to frugivory. *American Journal of Primatology*, *71*(2), 91-100.

Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour?. *Applied Animal Behaviour Science*, *102*(3), 163-188.

McNeilage, A., Plumptre, A. J., Brock-Doyle, A., & Vedder, A. (2001). Bwindi impenetrable national park, Uganda: Gorilla census 1997. *Oryx*, *35*(1), 39-47.

Meder, A. (1989). Effects of hand-rearing on the behavioral development of infant and juvenile gorillas (*Gorilla gorilla gorilla*). Developmental Psychobiology, 22(4), 357-376.

Metrione, L. C., Norton, T. M., Beetem, D., & Penfold, L. M. (2008). Seasonal reproductive characteristics of female and male Jackson's hartebeest (*Alcelaphus buselaphus jacksoni*). *Theriogenology*, *70*(6), 871-879.

Muller, M. N., & Wrangham, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *55*(4), 332-340.

Minitab 17 Statistical Software (2017). [Computer software]. State College, PA: Minitab, Inc. (www.minitab.com).

Novak, M. A., Meyer, J. S., Lutz, C., & Tiefenbacher, S. (2006). Deprived environments: developmental insights from primatology. Sterotypic animal behaviour: fundamentals and applications to welfare. 2nd ed. Wallingford, UK: CABI, 153-189.

Nowell, A. A., & Fletcher, A. W. (2007). Development of independence from the mother in *Gorilla gorilla gorilla*. *International Journal of Primatology*, *28*(2), 441-455.

Ogden, J. J., Lindburg, D. G., & Maple, T. L. (1993). Preference for structural environmental features in captive lowland gorillas (Gorilla gorilla gorilla). Zoo biology, 12(4), 381-395.

Parnell, R. J. (2002). Group size and structure in western lowland gorillas (Gorilla gorilla gorilla) at Mbeli Bai, Republic of Congo. *American Journal of Primatology, 56*(4), 193-206.

Peel, A. J., Vogelnest, L., Finnigan, M., Grossfeldt, L., & O'Brien, J. K. (2005). Non-invasive fecal hormone analysis and behavioral observations for monitoring stress responses in captive Western lowland gorillas (*Gorilla gorilla gorilla). Zoo Biology, 24*(5), 431-445.

Perry, S. F., & Gilmour, K. M. (1999). Respiratory and cardiovascular systems. *Stress Physiology*, 52-107.

Porton, I., & Niebruegge, K. (2006). The changing role of hand rearing in zoo-based primate breeding programs. In: Sackett, G. P., Ruppenthal, G., & Elias, K. (Eds.). *Nursery rearing of nonhuman primates in the 21st century*. Springer Science & Business Media.

Porton I, White M. (1996). Managing an all-male group of gorillas: eight years of experience at the St. Louis Zoological Park. In: Proceedings of the Regional Conference of the American Zoo and Aquarium Association, Denver, CO. p 720–8.

Quade, D. (1967). Rank analysis of covariance. *Journal of the American Statistical Association, 62*(320), 1187-1200

Remis, M. J. (1994). Feeding ecology and positional behavior of western lowland gorillas (*Gorilla gorilla gorilla*) in the Central African Republic. *Ph. D. thesis, Yale Univ.*

Robbins, M. M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour*, *132*(1), 21-47.

Robbins, M.M. (1996). Male-male interactions in mixed-sex and all-male wild mountain gorilla groups. *Ethology* 102:942–65.

Robbins, M. M. (2001). Variation in the social system of mountain gorillas: the male perspective. In Mountain gorillas: Three decades of research at Karisoke (pp. 29-58). Cambridge University Press.

Robbins, M. M. (2008). Feeding competition and agonistic relationships among Bwindi Gorilla beringei. *International Journal of Primatology*, *29*(4), 999.

Robbins, M. M., Bermejo, M., Cipolletta, C., Magliocca, F., Parnell, R. J., & Stokes, E. (2004). Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology, 64*(2), 145-159.

Robbins, M. M., Czekala, N. (1997). A preliminary analysis of urinary androgen and corticoid in male mountain gorillas. *American Journal of Primatology, 43*, 51–64.

Robbins, A. M., Gray, M., Basabose, A., Uwingeli, P., Mburanumwe, I., Kagoda, E., & Robbins, M. M. (2013). Impact of male infanticide on the social structure of mountain gorillas. *PLoS One*, 8(11), e78256.

Robbins, A. M., Gray, M., Uwingeli, P., Mburanumwe, I., Kagoda, E., & Robbins, M. M. (2014). Variance in the reproductive success of dominant male mountain gorillas. *Primates, 55*(4), 489-499.

Robbins, M. M., Robbins, A. M., Gerald-Steklis, N., & Steklis, H. D. (2005). Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank. *Behaviour*, *142*(6), 779-809.

Rosenbaum, S., Silk, J.B., Stoinski, T.S. (2011). Male–immature relationships in multi-male groups of mountain gorillas (*Gorilla beringei beringei*). *American Journal of Primatology 73*:356–365

Rosenbaum, S., Maldonado-Chaparro, A. A., & Stoinski, T. S. (2016). Group structure predicts variation in proximity relationships between male–female and male–infant pairs of mountain gorillas (*Gorilla beringei beringei*). *Primates*, *57*(1), 17-28.

Ross, M.R. Niemann, T., Wark, J.D., Heintz, M.R., Horrigan, A., Cronin, K.A., Shender, M.A., Gillespie, K. (2016). Zoomonitor (Version 1)[Mobile application software]. Available from https://zoomonitor.org.

Ross, S. R., & Lukas, K. E. (2006). Use of space in a non-naturalistic environment by chimpanzees (Pan troglodytes) and lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science*, *96*(1), 143-152.

Ross, S. R., Calcutt, S., Schapiro, S. J., & Hau, J. (2011a). Space use selectivity by chimpanzees and gorillas in an indoor–outdoor enclosure. *American Journal of Primatology*, *73*(2), 197-208.

Ross, S. R., Wagner, K. E., Schapiro, S. J., Hau, J., & Lukas, K. E. (2011b). Transfer and acclimatization effects on the behavior of two species of African great ape (*Pan troglodytes* and *Gorilla gorilla gorilla*) moved to a novel and naturalistic zoo environment. *International journal of primatology*, *32*(1), 99-117.

Ryan, S., Thompson, S. D., Roth, A. M., & Gold, K. C. (2002). Effects of hand-rearing on the reproductive success of western lowland gorillas in North America. *Zoo Biology*, 21(4), 389-401.

Sánchez, M. M., Noble, P. M., Lyon, C. K., Plotsky, P. M., Davis, M., Nemeroff, C. B., & Winslow, J. T. (2005). Alterations in diurnal cortisol rhythm and acoustic startle response in nonhuman primates with adverse rearing. *Biological psychiatry*, *57*(4), 373-381.

Schmidt-Reinwald, A., Pruessner, J. C., Hellhammer, D. H., Federenko, I., Rohleder, N., Schürmeyer, T. H., & Kirschbaum, C. (1999). The cortisol response to awakening in relation to different challenge tests and a 12-hour cortisol rhythm. *Life sciences*, *64*(18), 1653-1660.

Schwarzenberger, F. (2007). The many uses of non-invasive faecal steroid monitoring in zoo and wildlife species. *International Zoo Yearbook, 41*(1), 52-74.

Shutt, K., Setchell, J. M., & Heistermann, M. (2012). Non-invasive monitoring of physiological stress in the Western lowland gorilla (Gorilla gorilla gorilla): validation of a fecal glucocorticoid assay and methods for practical application in the field. General and comparative endocrinology, 179(2), 167-177.

Sicotte, P. (2001). Female mate choice in mountain gorillas. In: Robbins,M.M., Sicotte, P., Stewart, K.J. (Eds.), Mountain Gorillas: Three Decadesof Research at Karisoke. Cambridge University Press, Cambridge, pp.59–87.

Steele, R. E., Fried, J. & Bennett, C. (1993). In: The effects of a silverback western lowland gorilla on the behavior and spacing of females in a naturalistic enclosure, Proceedings of the American Zoo and Aquarium Association Annual Conference, pp. 312–318.

Stevenson, M. F. (1983). The captive environment: Its effect on exploratory and related behavioural responses in wild animals. In J. Archer & L. Birke (Eds.), Exploration in animals and humans. Berkshire: Van Nostrand Reinhold.

Stewart, K.J. (2001). Social relationships of immature gorillas and silverbacks. In: Robbins MM, Sicotte P, Stewart KJ (eds) Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, Cambridge UK, pp 184–213.

Stoinski, T. S., Czekala, N., Lukas, K. E., & Maple, T. L. (2002). Urinary androgen and corticoid levels in captive, male Western lowland gorillas (*Gorilla gorilla gorilla*): Age-and social group-related differences. *American Journal of Primatology*, *56*(2), 73-87.

Stoinski, T. S., Hoff, M. P., & Maple, T. L. (2001a). Habitat Use and Structural Preferences of Captive Western Lowland Gorillas (*Gorilla gorilla gorilla*): Effects of Environmental and Social Variables. *International Journal of Primatology*, *22*(3), 431-447.

Stoinski, T. S., Hoff, M. P., Lukas, K. E., & Maple, T. L. (2001b). A preliminary behavioral comparison of two captive all-male gorilla groups. *Zoo Biology*, *20*(1), 27-40.

Stoinski, T. S., Jaicks, H. F., & Drayton, L. A. (2012). Visitor effects on the behavior of captive western lowland gorillas: the importance of individual differences in examining welfare. *Zoo Biology*, *31*(5), 586-599.

Stoinski, T. S., Kuhar, C. W., Lukas, K. E., & Maple, T. L. (2004a). Social dynamics of captive western lowland gorillas living in all-male groups. *Behaviour*, *141*(2), 169-195.

Stoinski, T.S., Lukas, K.E., Kuhar, C.W. (2008). Current status of all-male and mixed-sex groups within the AZA population. In: Paper presented at the International Gorilla Workshop, Orlando, Florida.

Stoinski, T. S., Lukas, K. E., & Kuhar, C. W. (2013). Effects of age and group type on social behaviour of male western gorillas (*Gorilla gorilla gorilla*) in North American zoos. *Applied Animal Behaviour Science, 147*(3), 316-323.

Stoinski, T. S., Lukas, K. E., Kuhar, C. W., & Maple, T. L. (2004b). Factors influencing the formation and maintenance of all-male gorilla groups in captivity. *Zoo Biology*, *23*(3), 189-203.

Stokes, E. J., Parnell, R. J., & Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology*, *54*(4), 329-339.

UNEP-WCMC (Comps.) 2015. The Checklist of CITES Species Website. CITES Secretariat, Geneva, Switzerland. Compiled by UNEP-WCMC, Cambridge, UK. http://checklist.cites.org. Accessed on February 16 2016.

VanBruggen, M. D., Hackney, A. C., McMurray, R. G., & Ondrak, K. S. (2011). The relationship between serum and salivary cortisol levels in response to different intensities of exercise. *International Journal of Sports Physiology and Performance*, *6*(3), 396-407.

Walsh P, C Tutin, J Baillie, F Maisels, E Stokes and S Gatti. 2008. Gorilla gorilla ssp. gorilla. The IUCN Red List of Threatened Species 2008: e.T9406A12984261. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T9406A12984261.en. Accessed on February 15 2016.

Washburn, B. E., & Millspaugh, J. J. (2002). Effects of simulated environmental conditions on glucocorticoid metabolite measurements in white-tailed deer feces. *General and comparative endocrinology*, *127*(3), 217-222.

Watts, D. P. (1990). Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. *Zoo Biology, 9*:185–200.

Watts, D. P. (1992). Social relationships of immigrant and resident female mountain gorillas. I. Male-female relationships. *American Journal of Primatology, 28*(3), 159-181.

Watts, D. P. (1995). Post-conflict Social Events in Wild Mountain Gorillas (Mammalia, Hominoidea). I. Social Interactions between Opponents. *Ethology*, *100*(2), 139-157.

Watts, D. P. (2000). Causes and consequences of variation in male mountain gorilla life histories and group membership. In: Kappeler PM, editor. *Primate males: causes and consequences of variation in group composition*. Cambridge: Cambridge University Press. p 169–179.

Whitworth, J. A., Williamson, P. M., Mangos, G., & Kelly, J. J. (2005). Cardiovascular consequences of cortisol excess. *Vascular health and risk management*, *1*(4), 291.

Wielebnowski, N. C., Fletchall, N., Carlstead, K., Busso, J. M., & Brown, J. L. (2002). Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. *Zoo Biology*, *21*(1), 77-98.

Wilson P., & Cooper C. 2008. Finding the magic number. The Psychologist, 21, 866-867.

Wright, E., Robbins, A. M., & Robbins, M. M. (2014). Dominance rank differences in the energy intake and expenditure of female Bwindi mountain gorillas. *Behavioral Ecology and Sociobiology*, *68*(6), 957-970.

Yamagiwa J. 1987. Intra- and inter-group interactions of an all-male group of Virunga mountain gorillas. *Primates* 28:1–30.

Zhang, B. (2017). Consequences of early adverse rearing experience (EARE) on development: insights from non-human primate studies. *Zoological Research*, *38*(1), 7.

VITA

Kaylin graduated with her B.S. from Purdue University with a major in Biology and concentration in Animal Behavior. While at Purdue her fascination with zoo research began during her time as an African ape behavior monitoring intern at the Lincoln Park Zoo. Throughout her first Biology graduate program at Ball State University, she continued to maintain a collaborative position between the university and various zoos including the Indianapolis Zoo, Fort Wayne Children's Zoo and Louisville Zoo. Her thesis research revolved around the welfare implications of natural and non-natural enrichment on the behavior of zoo-housed orangutans. Since arriving at the University of the North Florida, she has continued to focus on research utilizing behavior as an indicator of welfare in zoo-housed apes at the Jacksonville Zoo and Gardens. She also worked a research fellow at the zoo where she acted as the primary investigator for several primate behavioral studies. Kaylin plans to publish her current research conducted on the behavior and physiology of multi-male heterosexual gorilla groups and go on to obtain a PhD in the field of animal behavior.