

May 2016

# Captive Chimpanzee Group and Individual Space Use in a Naturalistic Enclosure

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CAPTIVE CHIMPANZEE GROUP AND INDIVIDUAL SPACE USE IN A  
NATURALISTIC ENCLOSURE

by

Amanda Epping

A Thesis Submitted in  
Partial Fulfillment of the  
Requirements for the Degree of

Master of Science  
in Anthropology

at

The University of Wisconsin-Milwaukee

May 2016

## ABSTRACT

### CAPTIVE CHIMPANZEE GROUP AND INDIVIDUAL SPACE USE IN A NATURALISTIC ENCLSOURE

by

Amanda Epping

The University of Wisconsin-Milwaukee, 2016  
Under the Supervision of Professor Trudy Turner

Current research continues to identify the cognitive and social abilities of chimpanzees, as well as the imperative to provide a complex environment in captivity that allows them to practice and use their minds appropriately (Ross 2009). The goal of this research is to investigate how chimpanzee social relationships change based on the available amount of enclosure space in a captive setting. The project's study group is made up of six captive born chimpanzees housed in a naturalistic enclosure at the Lincoln Park Zoo in Chicago, Illinois. Data is taken daily as a part of a long-term study at the Lester E. Fisher Center for the conservation of great apes. Research has shown that choice is an important aspect of animal welfare. This study looks at the interindividual distance between dyads of chimpanzees and how the distance changes when the enclosure space changes. Multilevel analysis was used to create an expected pattern of distance between four different space conditions using both average distance and relative distance. The expected pattern shows the order of spacing across the different conditions, meaning the relative interindividual distance between two individuals is expected to be the largest

when the animals are locked inside and the smallest when the animals are locked outside. It was found that the animals do spread out further when they have a larger amount of space when looking at the average distance between dyads. When looking at the relative distance between dyads, it was found that the animals use a higher percentage of space when there is less available and dyads always follow the expected pattern of interindividual distance. Female dyads were shown to be the closest in this group. Dyad differences do occur across the four conditions and are discussed using known chimpanzee social patterns. Welfare implications and research showing how naturalistic enclosures promote natural behavior in captive settings is addressed.

Ross, S et al. (2009). Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. In *Applied Animal Behaviour Science*. 121:42-50.

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## **ACKNOWLEDGMENTS:**

First and foremost, I would like to thank my advisor, Trudy Turner. Thank you for the constant support and encouragement. I would also like to thank my committee members, Pat Gray and Fred Anapol for sharing their knowledge in statistics and for helping me with the organization of this thesis. I appreciate all of the time you three have spent talking through this with me and appreciate that you were always able to squeeze me in last minute when needed.

I would like to thank Lydia Hopper, Steve Ross, and everyone at the Lester E. Fisher Center for making this thesis possible. My education would not have been complete without the hands on experience I received as an intern under your supervision. Being around the staff at the fisher center was incredibly motivating and I appreciate all of the guidance and support over the years of interning there. I would also like to thank all of my fellow interns who helped collect the data used in this project.

Finally, I would like to thank my friends and family for the constant support over the last three years, and really over my lifetime. I was able to follow my dreams will continue to do so because of you. This thesis would not have been possible without the encouragement and patience you have shown me, I am forever grateful to be surrounded by such wonderful people.

## **Introduction**

Chimpanzees and gorillas are the two most common apes found in captive environments across North America (Fulk 2004). Chimpanzees and orangutans have been on display in captivity in Europe as early as the eighteenth century, but few specimens lived for very long (Maple 1979). Van Hooff wrote in 1973 that there was a “growing feeling in the last few years that the conventional methods of keeping great apes were not fully adequate” as they were still showing many anxious behaviors and having difficulty rearing offspring. Since then, research has led to many improvements in the husbandry of keeping great apes in zoos. Hosey (2005) proposes three reasons why it is important to understand the behavior of captive primates in zoos, including a way to enhance welfare, a way to promote a positive experience for zoo visitors, and a way to properly understand and interpret research coming from zoos.

Early research concerning apes in zoos focused on giving apes in captivity enough space. Clark (1982) and Wilson (1982) found that naturalistic enclosures and movable play things significantly improved welfare for captive apes. The current trend in captive environments is naturalistic enclosures that simulate captive apes and also promote a positive experience for zoo visitors. Ross and colleagues (2011) call for functional naturalism, where the structures not only look like wild environments, but also serve a similar purpose in promoting species-typical behavior for the apes. Choice has also been shown to promote positive behaviors in captive apes. Kurtycz and colleagues (2014) found that when captive chimpanzees had the choice to go to an outdoor enclosure there was an increase in arousal.

As zoos and sanctuaries continue to try to provide the animals with a species-typical life, information about their preferences and behavior in captive environments will be important in deciding how and where captive chimpanzees are going to live. This research aims to look at space use and how it affects individual dyads in a captive group of chimpanzees. The chimpanzees at Lincoln Park Zoo are presented with four different options for enclosure space. Locked inside and locked outside keep them in one area of their enclosure, and by the use of sliding glass doors they regularly have a choice either to go inside and outside as they please by one or two doors. This research will look at group and individual differences in the way the space is utilized throughout the different access conditions in a group of captive born chimpanzees socially housed at the Lincoln Park Zoo in Chicago, Illinois.

### **Group Living and Wild Chimpanzees**

Animals who live in groups are trying to find the balance between the maximum amount of benefit with the most manageable amount of cost. The size of a group is usually the result of a process that maximizes benefits while minimizing costs. Each environment will cause different challenges and animals have evolved behavioral strategies to reduce the costs of group living. An example of a behavioral strategy is the fission-fusion seen in chimpanzee populations. Traditionally, two models have been proposed to explain the variation in-group size seen in different environments, the socioecological theory and the ecological constraints model. These models make predictions on group size based on the distribution and female relationships in groups of primates.

Wrangham (1980) focused on feeding competition and female relationships as a starting point to make predictions on the adaptive significance of social organization in

non-human primates. This became the socioecological theory, which states that under conditions where food is limited, the frequency of agonistic interactions is expected to be high, especially among females (Sussman and Garber 2011). Low ranking females can experience a cost in reduced fitness, including decreased nutrition, fertility, or infant survivorship, and an increase in vulnerability to predators by foraging apart from other group members (Boinski et al 2000). Female food competition has traditionally been suggested as the ultimate evolutionary force influencing primate social organization.

Van Schaik (1989) modified Wrangham's model and suggested that predation risk was the ultimate factor forcing females to live in groups despite the costs of feeding competition. Van Schaik argued that predation risk puts a lower limit on group size, while within-group food competition sets the upper limit. Sterck, Watts, and Van Schaik (1997) expanded the 1989 model further by including social variables and defining possible social outcomes. Male behavior, habitat saturation, and the cost of dispersal were added along with predation and food distribution as a way to explain more of the observed variation seen across primate grouping patterns and social organization. Isbell (1991) and Isbell and Young (2002) further explored how the social and ecological costs of dispersal could act as an important factor in the formation of social groupings. They concluded that when food resources are clumped, group competition would occur, and when food was widely dispersed competition would not occur.

For species that are female bonded, the socioecological model requires that females live in groups when the benefits of cooperative resource defense outweigh the cost of in-group feeding competition. Females would be expected to bond with relatives to cooperatively defend access to priority food resources and large groups will be able to

outcompete smaller groups (Snaith and Chapman 2007). Non-female bonded species, including chimpanzees, would be expected to rely on high-quality, patchy resources and display short-term variation in group size as seen through the nature of their fission-fusion party formation.

The ecological constraints model has been commonly referred to in the literature as well to explain why primates live in groups (Chapman and Chapman 2000). This model suggests that group size is an outcome of daily travel costs. When food is patchy, larger groups will have to move more often as they will deplete patches quicker than smaller groups and have to travel more often fill their energetic needs. The model predicts that the cost of travel will show in the increased time and energy spent moving to food patches, and the decrease in time spent feeding and resting. If the costs are high and individuals in larger groups are required to travel further, then a decrease in individual fitness should be seen.

Chimpanzee party size is known to fluctuate based on receptive females in a party (Goodall 1986, Mitani et al 2002), food availability (Anderson et al. 2002), predation pressure (Boesch 1991, Goodall 1986), and demographic factors (Goodall 1986, Lehmann and Boesch 2004). Although chimpanzees live in a tightly bonded community where all members know each other, they split up into smaller sub groups (parties) that frequently change both size and composition (Boesch and Boesch-Ackermann 2000). Fission fusion has been suggested has a behavioral mechanism to overcome ecological variables, including feeding competition, and reduce agnostic in-group encounters.

New evidence testing the two models discussed is showing that social factors and ecological factors may be equally important when primates are weighing their option to

join or leave a group. As summarized by Sussman and Garber (2011:595), new research has shown that “agonism occurs at low frequencies among diurnal primates living in the same social group, agonism at feeding sites does not occur more frequently among female primates the form linear dominance hierarchies, and individuals in larger groups of and primates do not necessarily travel greater distances than those in smaller groups.” These findings do not support the ecological constraints model or the socioecological model. Sussman and Garber (2011) suggest that based on the available information, it is likely that the dynamics of social living, the opportunities for sub groups, and patterns of group fission set the limit on how much feeding competition will result in significant fitness costs.

Captive animals are faced with different social and ecological struggles than their wild counterparts, but the behavioral mechanisms would be expected to exist in captivity as well as in the wild. The chimpanzees in captivity show a preference for certain types of food and space within the enclosure. These areas can still be considered defensible, as higher-ranking members will still have priority access to the preferred items and space. If a limited amount of highly preferred space is available, dominant members should be able to monopolize it from low-ranking members. When the chimpanzees have access to a larger amount of space and the choice to spread out from each other, subordinate members would be expected to take advantage of this and use the space that dominant members are not in.

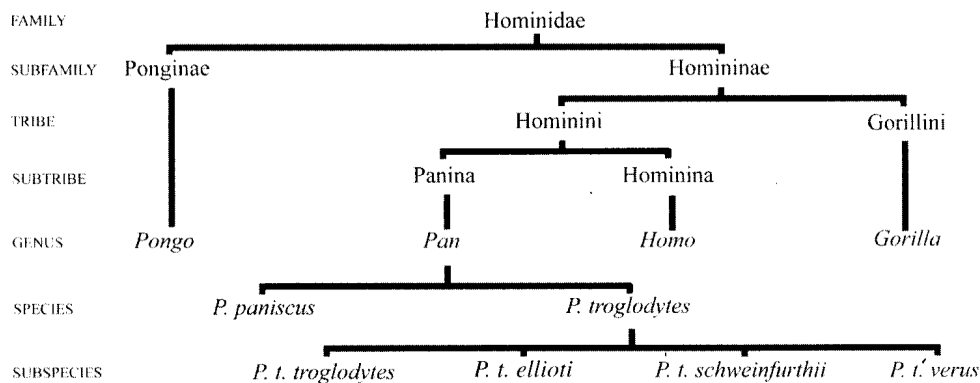
### **Key Questions of Research**

This study aims to investigate captive chimpanzee interindividual distances and social relationships in captivity. Specifically, the choice to go to a larger, outdoor enclosure will be examined to see how it changes the interindividual distances between group

members. Do the chimpanzees space out or stay close when more space is given? Do social relationships emerge when they have more space and a choice to spread out? The predictions of this research are that when the chimpanzees have access to a larger amount of space, via an outdoor yard, they will spread out further and social bonds will emerge based on proximity to other group members across different levels of available space. Because of the different access availabilities and large exhibit space, individuals can choose to interact socially with different individuals, and utilize different areas of their enclosure, ultimately improving their welfare. When high priority space is available, such as doorways or platforms, subordinate members should space out further to give dominant individuals access to the preferred space.

### **Natural History**

All of the African primates can be classified into two suborders and four families. Strepsirrhini holds the families Galagidae and Lorisidae. Lemurs, Haplorrhini holds the families Cercopithecidae and Hominidae (Groves 1993, 2001). Chimpanzees belong to the family Hominidae that includes all great apes and their fossil ancestors. African apes, humans, and fossil ancestors to these species belong to the subfamily Homininae (Figure 1). Hominoids, like cercopithecoids, have a tympanic bone structure and a dental formula of 2.1.2.3. (Fleagle 1988).



**Figure 1:** Recent taxonomy that puts humans, great apes, and ancestors all within the family Hominidae. Image from Stumpf 2011:343, following Groves 2010 and Mann and Weiss 1996.

Chimpanzees, bonobos, and humans are all together within the tribe Hominini. Following Groves (2001) bonobos and chimpanzees split from humans in the sub tribe Panina, while humans are in Hominina. Bonobos and chimps are united by the Genus *Pan*. Humans are alone in the species *Homo*, although there has been some debate as to whether *Pan* belongs under *Homo* as a subgenus (Goodman et al 1998) based on the chimpanzee and human line diverging between 6 million and 4 million years ago (Goodman et al 1998, Easteal and Herbert 1997). This early date has been debated and disputed, and is more often cited between 7 and 10 million years ago (White et al 2009) leaving chimpanzees and bonobos separate from humans in the genus *Pan*.

The genus and species of the chimpanzee is *Pan troglodytes*, and they are further split into four sub species based on genetic and morphological differences (Groves 2001, Grubb et al 2003). The four sub species are central African (*Pan troglodytes troglodytes*), East African (*Pan troglodytes schweinfurthii*), West African (*Pan troglodytes verus*), and the



fourth recognized group (*Pan troglodytes vellerosus*) is those from Nigeria and Cameroon (Groves 2001, Gonder et al. 1997).

Chimpanzees and bonobos diverged between an estimated 800,000 years ago and 2.7 million years ago. The split between western (*P. t. verus*) and central/eastern chimpanzees (*P. t. troglodytes* and *P. t. schweinfurthii*) is estimated between 500,000 years ago and 1.6 million years ago (Morin 1994). Bonobos were originally considered a sub species of chimpanzees based on skull morphology. In 1933, they were classified as a separate species (Coolidge 1933). The greatest genetic difference within a chimpanzee sub species is seen within *P. t. troglodytes* and the least within *P. t. verus* (Fischer et al. 2006).

Of all of the chimpanzee sub species, *P. t. troglodytes* is the largest and most sexually dimorphic in body mass (Stumpf 2011). Visually, facial patterns vary across the different subspecies. *P. t. verus* has a darker mask around the face and lighter skin tone on the rest of their face. *P. t. troglodytes* generally has a dark face that darkens to a deep black when adulthood is reached. *P. t. schweinfurthii* has a freckled face that darkens with age (Stumpf 2011). In contrast, bonobos are born with black faces and white tufts on the tail that do not disappear in adulthood as seen in chimpanzees.

### **Social Ecology of Chimpanzees**

Chimpanzees are distributed across diverse habitats in equatorial Africa (figure 2), including tropical rainforests and savannah woodlands (Stumpf 2011). Populations are known as far north as west Senegal, south to the Congo River, across northern Congo, and east of Lake Tanganyika, Tanzania (Stumpf 2011). They live in multimale/multifemale groups that range drastically in size from a small handful of individuals to an observed 150 individuals. Males generally stay in their natal groups and are the dominant sex. Females

consistently transfer across populations once they reach sexual maturity and have to establish initial relationships with the resident males and females (Pusey 1980). Research began with Jane Goodall in Gombe in the 1960s, and followed in West Africa the 1970s with Christopher Boesch in the Tai National Park, Ivory Coast and Yukimaru Sugiyama in Bossou, Guinea.



**Figure 2:** Distribution from the IUCN of wild chimpanzee home ranges. Darker shading on map indicates wild population range (Oates et al. 2008).

While aspects of behavior and ecology are similar across chimpanzee sites, substantial differences have been observed between populations. Studies showing the complexity of grouping patterns, behavior, and feeding ecology have shown differences even within the same sub species (Stumpf 2011). For example, Luncz and Boesch (2015) found 27 distinct cultural traits in adjoining chimpanzee communities that were not ecologically driven. The chimpanzees of Senegal present a unique opportunity as they face

similar ecological pressures as likely human ancestors did. Pruetz and Bertolani (2007) found that the chimpanzees living here were able to fashion tools in a way not seen by other populations to spear bush babies out of a tree.

The diet of wild chimpanzees is mostly frugivorous (Wrangham et al., 1998). Depending on scarcity and where the group is living, the range of plant species eaten by chimpanzees is highly variable. When food is scarce, chimpanzees will rely on low value foods and eat a wider variety of plants than they do when food is not scarce (Wrangham 1977). Animal protein is a small part of their diet, consisting of about 10% in some populations, less in others (Goodall 1986). Hunting has been observed in chimpanzee groups and colobus monkeys are the most commonly hunted species, seen being eaten 50% of the time that meat is being consumed by males in a Tanzania population (Wrangham 1977, Stumpf 2011). Overall, the diet of chimpanzees is approximately comprised of fruit (64%), leaves (16%), THV (7%), bark and misc. (4%), Prey (4%), flowers (2%), and seeds (3%) (Stumpf 2011). In Bossou, chimpanzees used tools for getting food about 16% of the time (Yamakoshi 1999), suggesting that in some populations tool use is important for survival.

Fission-fusion is a flexible social nature that chimpanzees, bonobos, and humans all have in common. During fission-fusion, smaller sub groups, or parties form and disperse for a period of time from the rest of the group. The parties frequently change both in members and size. Females are thought to make social decisions and consider feeding competition and generally males will try to follow swelling females (Anderson et al 2002). Parties can stay away from the group for a wide range of time, anywhere from part of the day to days at a time. It is often cited that estrous females or food availability are strong

determinants of party size in chimpanzees, and Mitani et al (2002) found that both of these factors operate together to produce the patterns seen in wild populations.

### **Hunting and Food Sharing**

Hunting and meat sharing are an important aspect of chimpanzee social life. Red colobus monkeys are the most common prey in every long-term site where they are sympatric with chimpanzees including Mahale and Gombe in Tanzania, Kenyaware and Ngogo of Kibale in Uganda, and Tai in Ivory Coast (Boesch et al 2002). Boesch (2002) reports in a study comparing hunting behavior across populations where red colobus live that chimpanzees are opportunistic, and they evaluate the situation when they hear prey rather than dive right in. Only in one population, Tai forest, have researchers reported chimpanzees actively searching for prey before starting to hunt (Boesch & Boesch 1989). In the Ngogo population (Kibale National Park, Uganda), adult males make almost all kills of monkey prey (Watts & Mitani 2002).

In Eastern populations, chimpanzees begin their hunt by testing the reaction of the prey. Boesch (2002) suggests this is because they have become experts in the capture of infant monkeys and want to make sure their targets will have infants in the group. In Gombe, chimpanzees test the prey by displaying on the ground or in trees and wait for a reaction from the monkeys. If the monkeys face or threaten them, they move on. In Mahale, chimpanzees watch the monkeys from the ground and observe their movements. They remain silent and position themselves to watch the behavior of the monkeys and if no one sees an opportunity to start a hunt they move on after around two hours (Boesch et al 2002).

Once a kill is made, dominant males are most likely to be in possession of the meat. They are most likely to share with their fellow male social partners and females in estrous, although they will share with anestrus females as well, probably to maintain support from resident females (Matsumoto-Oda 2002). Meat sharing is thought to be an important factor in maintaining cooperative social relationships (Nishida et al 1992, Watts and Mitani 2002). Males share reciprocally with other males they cooperate with, and with females both in estrous and anestrus. Beyond nutritional value, meat sharing appears to be an important contribution to maintaining social relationships within the group (Watts and Mitani 2002).

### **Reproduction and Life History**

High levels of male competition are directly associated with the low reproductive rates of female chimpanzees, which give birth once every five to six years (Goodall 1986, Boesch & Boesch 2000). Female chimpanzees have on average of a 35-day menstrual cycle. Estrus lasts about 10-15 days and is marked by a large pink swelling. Ovulation occurs in the second half of maximum swelling (Stumpf and Boesch 2005). When young females are still in their natal group they can go through a period of subfecundity, where conception is unlikely but they still show frequent swellings. It has been suggested that this is a strategy to avoid inbreeding (Pusey 1980).

Females initiate one-quarter to one-third of all mating attempts (Stumpf and Boesch 2006). Sex is often non-reproductive and females may mate with multiple males to avoid infanticide and increase social bonds (Stumpf & Boesch 2005). Females show preferences for mates and alter the frequency of mating depending on where they are in the ovulation cycle. They tend to be more promiscuous when conception is unlikely, and show a

preference for mates when conception is likely (Stumpf and Boesch 2006). There are four common types of mating reported in chimpanzees. Opportunistic mating occurs when females mate with many males in succession, consortship occurs when a male and female leave the group and travel together, possessive mating occurs when a male guards a female and prevents mating by other males, and extra-group mating, although rare, occurs when a female mates with individuals outside of the group (Stumpf 2011).

There is a strong seasonal influence on chimpanzee birth cycles (Boesch & Boesch-Ackermann 2000, Anderson et al 2000). Females appear to avoid heightened feeding competition through bigger parties by cycling in times of food abundance (Anderson et al 2000). Lower interbirth intervals in western populations could be due to more reliable food availability in dense forest (Wrangham 2002). Chimpanzees reproduce for a wider span of their lifetime, with decline starting at age 25, and approached zero at around the same time seen in humans when they reach menopause at age 50 (Matsuzawa 2010). Post reproduction lifespan is almost absent in wild chimpanzees, and uncommon in captive chimpanzees (Videan et al 2006).

A mother typically gives birth to a single infant. Weaning occurs at approximately age four, and mothers resume the menstrual cycle about 35 days after weaning. Once pregnant, the gestation period is around 230 days and babies are born at approximately 2 kg. During the first five years of life, the babies are extremely dependent on their mothers and mothers receive little to no help from males. Around the age of five, juvenile females start to spend more time with their mothers taking care of younger siblings and learning tool use for termite fishing (Lonsdorf et al 2004). Male juveniles begin to associate more

with adult males patrolling the periphery of the territory and following females in estrous (Matsuzawa 2010).

## **Social Relationships**

Social hierarchies and politics are a large part of chimpanzee interaction. Males are the philopatric sex and they form strong social bonds with each other called coalitions. Coalitions are defined as two or more individuals cooperating to direct aggression toward others (Mitani 2009). While male/male coalitions are common, they can change rapidly, causing disturbances in the group dynamics (de Waal 1982). Dominance is important for male chimpanzees because of a higher successful offspring rate for dominant males and long interbirth intervals for females (Boesch et al 2006). Male chimpanzees strive for dominance and form linear hierarchies while striving for the alpha male spot (Newton-Fisher 2004). In order to become the dominant male of the group, support is needed from resident females (de Waal 1982). When females begin to support a different male, there is often a takeover situation between dominant and subordinate males (de Waal 1982).

Male coalitions can endure over long periods and are crucial for a male to maintain his spot as the alpha male. Dominant males have been reported to cede matings to lower ranking males who help them maintain their position as alpha (Nishida 1983). Mitani (2009) reports that male dyads in Kibale National Park in Uganda that have the longest relationships also have the most reciprocal grooming relationships. Male relationships that are strong in one year have been reported as a strong predictor in subsequent years (Mitani 2009), and all males were reported to have at least one enduring social relationship with another male.

While males are known to cooperate with one another, they need to keep social tensions in check as well. Low ranking males have to attempt climbing in rank as they reach sexual maturity. They do this by displaying their strength to the group and hope to gain support for the resident females. These displays by males are often violent and aggressive. If a subordinate male begins to win conflicts with the dominant male more frequently, he can garner support from the females and eventually challenge the dominant male for his position. Once the conflict is over, it is common for reconciliation to be seen in chimpanzees where the winner will embrace or touch the loser to prevent long-term harm in the social relationship (Wrangham et al 2001).

Female relationships have proven to be more difficult to understand than male relationships. Originally considered weak (Goodall 1986, Wrangham 1979), current research is showing that females can be more bonded than originally assumed. For example, Wakefield (2013) has reported that females may indeed form differentiated social cliques that are stable over time, and Gilby and Wrangham (2008) have reported female dyads with grooming rates as high or higher than closely bonded males. Relationships between females are expected to vary with the levels of resource competition. If there is less available quality feeding space available, aggression will be higher among females. Dominant females show less variation in weight across seasons showing they are able to maintain normal feeding habits, and thus higher reproductive success, across seasons (Pusey et al 2005, Mitani 2009).

The ultimate goal for females is for their offspring to survive to sexual maturity, and in order to be successful females need to compete for space, food, and opportunities to reproduce (Mitani 2009). In some populations, when females emigrate to a new group,



they need to secure a core area where they will be able to find quality food at a consistent rate (Thompson et al. 2007). High-ranking females who have priority to high-ranking areas will try to monopolize these areas from low-ranking and transfer females (Pusey & Schroepfer-Walker 2013, Miller et al 2014). Foerster (2015) found that females from Gombe living in neighboring core areas groomed in direct relation with how much their core areas overlapped. However, Lehmann and Boesch found that females in the Tai Forest overlap in their core areas, but it does not relate to the females they associate with at a high rate. In eastern populations of chimpanzees, females spend a substantial amount of time alone foraging with their offspring (Murray et al 2007), likely due to increased resource competition (Wrangham 1979).

Other populations (see Lehmann & Boesch 2005) have found that all females use the entire home range and do not form distinct neighborhoods or monopolize areas long term. If chimpanzees are living in an area where the potential for conflict is high, social relationships between females may be to reduce conflict by forming friendships. Lehmann and Boesch (2008) found that females may use different kinds of social investments to achieve different goals, long-term associations to decrease competition by creating tolerance toward certain individuals and reducing aggression and short term grooming bouts as a flexible way to re-establish relations after periods of absence and after conflict.

Relationships between males and females also vary across populations and individuals. Short-term bonds could be formed for reproductive purposes. Party size increases when estrous females are present because males know they can increase their chance for offspring by being around swelling females. Relationships are more common between males and cycling females, and males who maintain a relationship with females

when they not in estrous have a better chance to copulate when they are in estrous again (Matsumoto-Oda 2002). Cycling females, regardless of current estrous status, have been shown to receive grooming and a share of meat more often than non-cycling females (Matsumoto-Oda 2002).

## **Cognition and Culture**

Chimpanzee cognitive abilities are complicated and still debated. Captive studies have shed light on what chimpanzee minds are capable of, but cannot fully replicate the ecological pressures of living in the wild. Wild studies are difficult as researchers are not able to get the full picture and know what is socially learned versus a genetic or environmental factor. The debate starts with whether the differences seen across chimpanzee populations are cultural, or genetic and environmentally influenced. It is generally accepted in the scientific community that chimpanzees do participate in social learning.

Shortly after potato washing was reported by macaques on Japan's Koshima Islet, Jane Goodall (1973) suggested that many of the behaviors exhibited by chimpanzees at Gombe were cultural variants, clearly distinct from other field sites. Whiten et al (1999) noted that some of the differences between communities represented alternative versions of otherwise similar patterns. Chimpanzees from the Tai forest in the Ivory Coast use a short stick to fish ants from their nests, while those from Gombe use a much longer stick and more efficient bimanual technique to achieve the same goal.

Generally, culture in primates is defined as behaviors that are specific to members of a group, and transmitted via some form of social learning (Caldwell and Whiten 2011). The first part of the previous statement can be explained through the different styles of tool

use that show uniformity while also showing an obvious variability. Social learning is more difficult to assume in the wild because while something could be socially learned, it difficult to rule out the behavior being caused by geographic variation (Galef 1990). Chimpanzees show the ability for innovation and manufacturing tools for tasks that make daily life easier, and some researchers have suggested a mixed interplay between environmental influences and social influences (Humble 2011).

Whiten (2011) reports that each chimpanzee community displays its own cultural profile. Immigrating females are the likely bearers of cultural variants not yet known locally in the communities they transfer too. An example of this can be seen when Matsuzawa (Biro 2003) introduced novel nuts into a community where hammer stones are used to crack nuts. One female was quick to crack the novel nuts, and after several years the majority of the population was cracking the novel nuts. A second example can be seen with one immigrant female adapting existing grooming techniques and eliciting adaption from residents who frequently groom with her (Nakumara 2004).

While chimpanzees and humans have showed similar growth in the brain after birth (Matsuzawa 2010), humans have shown less genetic heritability in the cerebral cortex (Gomez-Robles et al 2015). Chimpanzees and humans show similar physical development, but humans show greater plasticity can are more likely to be influenced by environmental influences, setting humans apart from chimpanzees when it comes to cultural evolution. Tomasello and Call (2010) have suggested that chimpanzees understand that others see, hear, and know things. Chimpanzees also understand others as goal-directed agents who also perceive the world in order to devise behavioral strategies for meeting those goals. When chimpanzees make decisions, those decisions are affected by what other individuals

are around and what they are likely to do (Tomasello and Call 2010). Lower ranked individuals have to find strategies to gain access to food and higher ranked individuals in order to survive and climb up in the hierarchy of the group.

### **Zoo-Based Research on Space Use**

Early research focused on giving apes in captivity enough space. Clark et al. (1982) recorded the behavior of a small group of chimpanzees before and after their translocation from a laboratory to a naturalistic island habitat. After 22 weeks on the man-made island, stereotyped and self-directed behaviors were dramatically less evident while their overall level of activity increased. Wilson (1982) reported that it was not the amount of space that really counted to the apes well-being, rather, it was the objects within space that improved welfare. In this study, activity was highly correlated with the number of group members and the presence of movable playthings. While early studies in captive welfare focused on giving the apes more usable space, further research is showing that beyond movable objects, the space itself has to be complex enough to stimulate captive apes.

Enclosures with a naturalistic feel to both the public and the apes that inhabit them are the current standard. Naturalistic enclosures have shown a decrease in stereotypical behaviors and positive effects on rates of aggression and affiliation (Clark et al 1982, Maple and Finlay 1986). In 2011, Ross wrote that the physical features and the environment complexity of captive environments are equally important as the total amount of space. Adult chimpanzees in captivity have shown a preference for specific areas (Ross et al 2011), and when there is an increase of enclosure perimeters and climbing structures, there is an overall increase in the use of available space used within the enclosure (Riss and Goodall 1976).

Ross and colleagues (2011) call for functional naturalism, where not only do the structures look like natural habitats, but they also serve a similar purpose, such as elevated resting sites. The current study site at the Regenstein Center for African Apes (RCAA) in Lincoln Park Zoo was built using the principles of functional naturalism, where data looking at structural preferences of the primates was used to create natural looking and functional exhibits (Ross et al 2011). This new building influenced the spatial distribution of the chimpanzees and gorillas, yet there has not been in depth research about how the choice affects their social relationships within the groups (Ross 2009).

## **Methods and Housing**

The Lincoln Park Zoo is located in Chicago, Illinois. It is a free zoo open to the public 365 days a year. Within the Zoo there are five research centers, The Alexander Center for Applied Population Biology, the Davee Center for Epidemiology and Endocrinology, the Populations Wildlife Management Center, The Urban Wildlife Institute, and the Lester E. Fisher Center for the Study and Conservation of Apes (Fisher Center). The research in this thesis was carried out at the Fisher Center within the zoo through an ape behavior internship. Data are collected at the Lincoln Park Zoo year round, Monday through Friday from 10am until 5pm. Interns participate in two long-term studies, a behavioral monitoring study that looks at individual's behavior and a social spacing study that looks at group space use and spatial cohesion. While studies have been done looking at the effects of naturalistic enclosures and space use in nonhuman primates, less research has been done on how the social relationships between individuals change given a choice between space availability in captivity.

Six captive-born adult chimpanzees, socially housed at the Regenstein Center for African Apes (RCAA) at the Lincoln Park Zoo, Chicago, IL, were the subjects for this study. The group (table 1) included two males and four females (average age: 20.23 years, range: 14-29 years). The group was housed in a publicly viewed exhibit with a large indoor dayroom (408.4 m<sup>2</sup>) and outdoor yard (2011.7m<sup>2</sup>). Photos of enclosure can be found in (appendix A). When weather permitted (>4 °C) the group was given the choice to their outdoor yard or to stay indoors by use of two 6m tall sliding glass doors. Data were taken for a one-year period from January 3, 2014 to December 30, 2014, Monday through Friday from 10am to 4:30pm.

ID:	Sex:	Age (Jan. 1 <sup>st</sup> 2014):
Hank (Ha)	Male	23
Optimus (Op)	Male	14
Chuckie (Ch)	Female	14
Nana (Na)	Female	19
Kathy (Ka)	Female	23
Cashew (Ca)	Female	29
Group	2M/4F	20.3

**Table 1:** Name identification, sex, and age for study group housed at Lincoln Park Zoo, Chicago IL

The indoor enclosure consisted of a deep mulch substrate for the ground, multiple concrete and deadfall trees, steel bamboo shoots, and synthetic vines that created a natural and complex environment. Elevated platforms and nesting areas were also built into the enclosure and added further opportunities for climbing and choice for nesting on the ground or at an elevated area. Temperature was kept at approximately 21°C inside. The ceiling was 10m high and housed several mesh panels that the chimpanzees could climb and hang from. These mesh panels were also along the wall in places and on the sides of

one large platform. Mesh panels served as a gateway for interaction from keeper or researcher to the apes and they separated the enclosure and management areas. The outdoor yard had natural grass and vegetation to the Chicago area as the floor, and consisted of the same type of climbing structures as the indoor yard. A mesh fencing which the chimpanzees were able to climb and hang from throughout the entire space encased the outdoor yard.

The wall between the outdoor yard and indoor enclosure is glass and consists of five 6m high and approximately 2m wide glass panels. The 2 panels on the ends were slide open and gave the group access to the outdoors (photo 1, 2, 3). When the doors were shut the group was still able to see their outdoor yard. There was an off exhibit holding area that the apes voluntarily entered for approximately 2 hours each day for exhibit maintenance and noninvasive cognitive and behavioral research. There were entrances to the off exhibit holding area from both the indoor and outdoor yard and they were opened at the discretion of the zoo keeping staff.

Data used for this study was collected by the group scan technique (for detailed description, see Altmann 1974), which records each individual's location within the exhibit (within a within a  $0.3 \times 0.3\text{m}^2$  squared grid), proximity to other group members, and elevation in two-meter intervals. Location and height were recorded for each individual in the group every minute during 30-minute sessions on a birds-eye digital map of the enclosure (appendix C). Height is recorded in 5 levels. Level 0 is recorded when the individual is on the ground level, and not sitting on anything with a height over 2.54cm. Levels 1, 2, 3, and 4 are recorded in 2m intervals. Level 4 is also recorded when any individual is higher than 6m.

The independent variables that were taken during each follow were weather, temperature, crowd size, crowd activity, access to off exhibit holding, and access to outdoor yard (locked in, locked out, access with one door, access with two doors). In this current study, the variables analyzed were each individual's location, height, and whether access was listed as locked inside, locked outside, access with one door, or access with two doors.

## **Analysis**

Only data when at least half the group was visible for more than 50% of the session was used in this study. All observers were required to pass an inter-observer reliability test with 85% reliability with an experienced researcher to ensure all data are being taken and recorded consistently. 581 sessions were included in this study amounting to 3,486 total follows and 104,580 total minutes of data. Distance between each dyad (pair of individuals) in the group (15 combinations) is averaged for the 30-minute session and includes both distance and height. For example, two individuals could be in the same location square on the grid, but still be counted as 6m apart based on their height intervals.

First, mean differences for the entire group was compared across the access points to determine whether there was a difference in the average spacing of the group as a whole. Locked inside (408.4 m<sup>2</sup>) is when the chimpanzees were locked inside the indoor enclosure and did not have access to the outdoor space by use of the sliding glass doors. Access with one door meant that one of the sliding glass doors was open allowing the chimpanzees to go outside. Access with two doors meant that both sliding glass doors are open and the chimpanzees have access to go outside in two ways that are not next to each other. Total space (2420.1m<sup>2</sup>) for access with one door and access with two doors was the same, but two doors allows for a second path outside. Locked outside meant that the



chimpanzees were locked in their outdoor enclosure (2011.7m<sup>2</sup>) and could not come inside by use of sliding glass doors.

Interindividual distances differed by access condition. A multilevel analysis was run allowing state to predict average distance and allowing the coefficients to differ in different dyads. A random slope intercept model was created that allowed the dyads to differ at the baseline level. The baseline level created suggested that the best predictor of relative distance was the mean of relative distance within dyads. Dyads interindividual distances were calculated and compared to check that they all fit the expected pattern of distance. The expected pattern of distance shows the order in which the dyads are expected to spread out based on what space is available. Dyads that do not follow the pattern and dyad-by-dyad differences across different available space will be discussed using known chimpanzee social patterns. Distance was corrected for relative distance using the interindividual distance between a dyad and dividing it by the amount of space available in the recorded condition. Dyad-by-dyad differences will be confirmed through a Kruskal-Wallis rank test. The locked in condition will be the baseline for the tests, locked out will also be tested as a baseline to test whether there are differences between the three times of open conditions (locked out, access with one door, access with two doors). All analysis was run in R-Studio (R Core Team 2013).

## **Results**

The chimpanzees were shown to space out further from each other in the open conditions when looking at average distance, and the open conditions did not differ significantly. When interindividual distance was corrected to relative distance based on available space, it shows that the chimpanzees use a higher percentage of the space when

they are locked inside. There are significant dyad-by-dyad differences throughout different space conditions.

### **Group Spacing**

Mean average distance shows that the group distances differ across the four conditions (table 2). The mean distance is highest for the access with two doors condition, and access with one door interestingly falls below the locked out condition even though more available space is available with one door open. Baseline levels were determined for each dyad by looking at average distance regardless of access condition.

Condition	Mean Group Distance (m)
Locked In	4.83
Locked Out	7.41
Access: 1 Door	6.53
Access: 2 Doors	7.49

**Table 2:** Group means across access conditions.

Dyad    Mean Average Distance(m) Across All Conditions

CaNa	3.61
ChKa	4.47
KaNa	4.92
CaKa	4.95
NaOp	6.20
ChNa	6.21
CaCh	6.25
HaOp	6.26
KaOp	6.27
CaOp	6.40
ChOp	6.60
HaKa	6.68
CaHa	6.70
HaNa	6.88
ChHa	7.07

Cashew and Nana appear to be the closest bonded dyad by looking at mean average distance, and Hank appears to space out the furthest from group members. The top four dyads with the smallest average interindividual distance are all female/female dyads. The only male/male dyad falls in the middle of the group. A fixed effect was used to predict average distance from access condition with random dyad intercepts. An ANOVA test showed that access condition does explain variation in the distance between dyads ( $p = 0.0$ ), and average distance is not the same across different conditions.

Using the condition locked in as a baseline model, a pattern of distance across access different amounts of space was estimated. Expected pattern refers to the order of distance, for example the expected pattern of distance in table 3 means the animals should space out further in the order of locked in, access with 1 door, locked out, and the largest distance should be access with 2 doors. The pattern (table 3) shows that that locked in is significantly different than the three open conditions. By a very small margin (difference of .08), access with two doors is predicted to be when the animals will spread out the furthest.

This is also the condition that allows for the maximum space (2420.1m<sup>2</sup>) and choice with two doors.

State	Lower CI	Estimate	Upper CI
Locked In	4.33	4.83	5.32
Access: 1 Door	5.96	6.53	7.10
Locked Out	6.85	7.41	7.97
Access: 2 Doors	6.80	7.49	8.17

**Table 3:** Estimate represents the expected pattern of average distance for individual dyads based on the random slope intercept model with upper and lower confidence intervals.

The chart below (table 4) shows the dyads and their average interindividual distance compared to the model on the top row. Six dyads do not follow the expected pattern, Cashew and Nana, Kathy and Chuckie, Hank and Optimus, Cashew and Hank, Hank and Kathy, and Hank and Chuckie. There is not significant difference in the open conditions, so the difference is very small.

Dyad	Locked in (m)	1 door (m)	Locked out (m)	2 doors (m)
<b>Expected</b>	4.83	6.53	7.41	7.49
<b>CaNn</b>	3.02	4.04	5.65	4.12*
<b>NnKy</b>	3.50	5.65	6.70	6.84
<b>CaKy</b>	3.78	5.55	6.27	6.51
<b>KyCh</b>	3.83	4.68	6.15	5.30*
<b>NnCh</b>	4.68	6.76	7.71	8.50
<b>NnOp</b>	4.77	6.98	7.06	8.17
<b>CaCh</b>	4.83	6.80	8.14	8.28
<b>KyOp</b>	4.87	7.28	6.90	8.04
<b>CaOp</b>	5.03	7.27	7.87	8.11
<b>HaOp</b>	5.27	6.76	7.73	7.55*
<b>ChOp</b>	5.30	7.70	7.39	8.10
<b>CaHa</b>	5.73	6.94	8.80	8.07*
<b>HaKy</b>	5.77	6.95	8.21	7.99*
<b>HaNn</b>	5.78	7.08	7.98	8.71
<b>HaCh</b>	6.24	7.54	8.56	8.06*

**Table 4:** Expected outcome and dyad means across access conditions. \* = Dyads that to not fit the expected pattern.

To create a second baseline model, average distance was converted into relative distance by dividing the mean distance by the amount of space available in each access condition. Baseline models were created using a random intercept and random slope multivariate analysis using dyads as the fixed effect. An ANOVA test was used to determine that a random slope model was the best predictor of relative distance across conditions (table 5). The pattern (referring to the order of expected distance) in this table was compared to dyads to determine if the entire group follows the predicted pattern.

State	Lower CI	Estimate	Upper CI
Locked In	10.60	11.82	13.03
Access: 1 Door	2.42	2.70	3.39
Access: 2 Doors	2.80	3.09	3.39
Locked Out	3.20	3.68	4.16

**Table 5:** Estimate represents the expected pattern of relative distance for individual dyads based on the random slope intercept model with upper and lower confidence intervals.

The dyads use a higher percentage of space when they are locked in. Even though they have less space available, they use more of the total enclosure space. Access with one door, access with 2 doors, and locked out all significantly differ from the locked in condition. The three open conditions do not significantly differ from each other. All dyads follow the expected pattern when distance is corrected to relative to the available space (table 6).

Dyads	Locked in (m)	1 door (m)	2 doors (m)	Locked out
<b>Expected</b>	11.82	2.70	3.09	3.68
<b>CaNn</b>	7.39	1.67	1.70	2.81
<b>NnKy</b>	8.56	2.33	2.83	3.43
<b>CaKy</b>	9.25	2.30	2.69	3.12
<b>KyCh</b>	9.38	1.94	2.19	3.06
<b>NnCh</b>	11.47	2.79	3.51	3.83
<b>NnOp</b>	11.69	2.88	3.38	3.51
<b>CaCh</b>	11.82	2.81	3.42	4.05
<b>KyOp</b>	11.93	3.01	3.32	3.43
<b>CaOp</b>	12.31	3.01	3.35	3.91
<b>HaOp</b>	12.91	2.79	3.12	3.84
<b>ChOp</b>	12.97	3.18	3.34	3.67
<b>CaHa</b>	14.02	2.87	3.33	4.34
<b>HaKy</b>	14.13	2.87	3.31	4.08
<b>HaNn</b>	14.14	2.93	3.60	3.97
<b>HaCh</b>	15.28	3.12	3.33	4.25

**Table 6:** Dyads mean distance compared to the expected pattern. All dyads follow expected pattern.

The analysis was run again using the locked out condition as the baseline and removing the locked in condition to determine if locked out, access with one door, and access with two doors differed significantly when locked in was removed as a condition. The results showed that the animals use more relative space when locked out compared to access with one door and access with two doors (table 7).

State	Lower CI	Estimate	Upper CI
1 door	2.46	2.699	2.93
2 doors	2.81	3.094	3.38
Locked out	3.42	3.682	3.94

**Table 7:** Relative distance estimates and confidence intervals when locked out is used as the baseline model. The animals do use more relative space when locked out, which is in line with the previous model that when less space is available the animals will use more of the space.

### Dyad Differences

Dyads were compared across different access points using a Kruskal-Wallis test for significance. All dyads significantly differed in their distance between locked in and locked out, locked in and one door, and locked in and two doors. There is dyad variation in the other 3 access combinations (one door and two doors, one door and locked out, two doors and locked out). The charts above show the dyads ranked in order from smallest interindividual distance at the baseline level to highest. (Table 6 and 4). Tables for each dyad can be found in appendix B that show their mean average distance across the four different access points, the coefficients from a linear regression model showing the difference in space between the baseline (locked in) condition and the other three, and the results of a Kruskal-Wallis post-hoc test showing which conditions have significantly different interindividual distances for each dyad (true = distances differ, false = differences do not differ).

Female/female dyads tend to have the smallest interindividual distances across the access conditions. The dyads that include one or both of the two males in the group regularly show a larger interindividual distance. The dyad with the consistently smallest



interindividual distance is females Cashew and Nana. Hank and Chuckie show the largest interindividual distance. Dyads that differ across the open access conditions include Cashew and Chuckie, Nana and Chuckie, Hank and Nana, Nana and Kathy, Hank and Cashew, and Nana and Cashew. These are of interest because all of these dyads include high ranking (Hank, Nana, Cashew) and/or bottom ranking (Chuckie) members of the group.

## **Discussion**

The chimpanzees at Lincoln Park Zoo have shown a strong preference for certain areas of their available space in the captive setting (Ross et al 2011). Further, they have shown increased welfare by having a choice to go outdoors (Kurtycz et al 2014). This research attempts to take a further look about how welfare and different options of choice and relative space change the dynamics of a group of highly social primates by looking at social relationships that emerge when the choice to spread out is given. If the animals choose to stay in close proximity to each other and commonly choose the same social partner or nearest neighbor, it can be assumed that strong social bonds exist within this captive group and that species-typical social relationships emerge in captive settings as well as wild groups.

This study examines the space use of a group of captive chimpanzees and looks at how different dyads choose to distance themselves based on how much space is available. Space and choice studies in primates are crucial in understanding size and access options in exhibit design to ensure animals in captivity can exhibit species-typical behavior. Chimpanzees are a dynamic species with advanced social capabilities. Captive

chimpanzees should be given enough quality space to distance themselves and choose social partners based on individual needs.

Choice is an important aspect in animal welfare and a lack of choice has been shown to increase abnormal and stereotypical behaviors (Maple and Finley 1986). A substantial amount of literature has shown for many animals in captivity, providing some choices relating to daily routines (food, enrichment, environment, social partners) can show an increase in of species-typical behavior. For example, Forthman et al (1992) found that when bears in zoos were given feeding enrichment rather than simply being fed, stereotypical behavior decreased and activity increased. Buchanan-Smith and Badihi (2012) found that for captive marmosets, the choice to control the light and heat in a captive environment improved welfare by lower levels of scent marking and calmer activity patterns.

Chimpanzees in captivity have shown a preference for vertical space, mesh barriers, corners and doorways, and avoidance of open spaces (Ross and Lukas 2006, Traylor-Holzer and Fritz 1985). Chimpanzees at Lincoln Park Zoo have been reported to spend approximately half of their time in only 3.2% of their available space and approximately a third of their time outside (Ross et al 2011). They are selective of their space showing how important quality is over the quantity of space. It has been suggested that high-ranking members of a group of captive chimpanzees could use preferred areas to control other individuals in the group (Ross and Lukas 2006). Multiple points of access to adjacent areas and different levels of vertical space are encouraged to ensure that high-ranking individuals cannot restrict the movement of low-ranking individuals.

Ross and Lukas (2006) discuss areas near doors being preferred areas in captive chimpanzee groups. The results from this research show that when one door or two doors are open, dyads are closer together (relative distance) than when they are locked outside, despite having more space with the choice to go inside or outside. If doorways are highly preferred areas, it makes sense that the animals would be closer together when they are open, as they should want to be as close to the preferred area as possible. This could account for the six dyads that do not follow the pattern seen in table 4. Hank is the dominant male in this group of chimpanzees. Table 6 shows the dyads ranked in order from smallest interindividual distance to largest when they are locked in. When table 6 is sorted by one or two doors, dyads that involve Hank rise in the rank to the middle of the pack. This could be because when the doors are open, the chimpanzees want to use them and be near them regardless of who else is near by.

In 2014, a study was conducted at the Lincoln Park Zoo that looked at behavioral differences of chimpanzees and gorillas when they had a choice to go outdoors and remained indoors compared to when the apes did not have the choice to go outside (Kurtycz et al 2014). They found that chimpanzees showed more frequent and self-directed behaviors while gorillas produced lower levels of object manipulation and feeding. The 2014 study compared the apes' behavior in different conditions of choice and found that chimpanzees demonstrate higher arousal when they are offered a choice, but they apes were always observed in the same size enclosure. The current study will add to this research and look at how space in addition to choice affects the group of chimpanzees at Lincoln Park Zoo when they have a choice to spread out.

The analysis showed that chimpanzees spread out more when more space is available, but use more of the relative space when they are confined in a smaller area (locked in). The use of more relative space use shows the importance of space that is not only large enough, but complex enough to offer the apes what they need. At the Lincoln Park Zoo, the Regenstein Center for African Apes was designed based on preferences seen in the captive apes living in the old ape house. The natural terrain confines what is possible in the outdoor space, but the indoor space at the RCAA was designed with all the preferences reported previously in mind (Ross et al 2011). This could partially account for the higher percentage of space used in the locked in condition seen in this research. The chimpanzees used more of the relative space available when locked inside.

Apes have shown preferences for areas in exhibits (Stoinski et al 2001, Ross et al 2011) and higher ranking individuals may get priority to higher desired areas, forcing subordinates to move elsewhere (Fretwell 1972, Sutherland and Parker 1985). This study predicted that apes would use more space when more space was available and that social relationships would emerge based on interindividual distances. Female dyads have the smallest interindividual distances across the access conditions. While originally considered weak, female relationships are more recently being reported to be comparable to male coalitions in wild populations (Wakefield 2013, Gilby and Wrangham 2008). Cashew and Nana exhibit the smallest interindividual distance across all access conditions. The only male/male dyad in this study does not fall in the top half of smallest interindividual distances, highlighting female relationships when there is less competition and no immigrating group members.

Mitani (2009) reports that female chimpanzees compete for space, and high-ranking individuals can exclude low-ranking individuals from high-quality areas. Competition between females is seen more often when new females immigrate into communities and attempt to form initial relationships with residents (Mitani 2009). In a captive setting, there is plenty of food and space to go around, but there very well may be areas that are more desirable to spend the day than others and more appetizing food piles laid out by the zookeepers. Cashew and Chuckie exhibit the greatest interindividual difference between female dyads and they also show the greatest age difference between group members. When both doors are open, Nana and Cashew both increase their distance from Chuckie compared to when they are locked inside. Low-ranking Chuckie may be excluded by high-ranking Cashew and Nana when more space becomes available. They are okay being near when space is limited, but with an option to spread out they choose to do so.

Hank, the dominant male, demonstrates the largest interindividual distance from the four females in the locked in condition. As the dominant male, Hank would have priority to any space he wants to occupy. When less space is available, the females appear to avoid Hank more than when there is more space available. Highly desirable areas are closer together inside, and Hank's presence could cause the females to avoid the areas he is in more frequently when locked inside. When locked outside or access with one or two doors is granted, Hank's relative interindividual distances between group members decreases (table 6).

Chimpanzees are not only selective of the space they use, but also who they will share their space with. This research adds to the knowledge by showing dyads with closer average distances than others. Closely bonded female dyads Cashew/Nana and

Kathy/Chuckie show a preference to have the same nearest neighbor no matter how much space is available. The difference between dyads also shows that low-ranking members will avoid high-ranking members when needed. The dyad Hank/Chuckie and Cashew/Chuckie reflect this. Ensuring high amounts of quality space should reduce conflict over preferred areas in captive settings. The Kruskal-Wallis (appendix B) test showed that all dyads have significantly different distance in the locked in and all three open conditions. There are dyads that differed in the three open conditions as well, but no obvious pattern emerged.

In order to maximize animal welfare, measuring how animals choose to utilize their space is way to determine both positive and negative aspects of their captive environment. Space use is not only influenced by environmental factors, but social and biological factors as well (Ross et al., 2009). Because chimpanzees have such a complex social structure and are cognitively advanced, housing them in a way that does not cause stress and abnormal behavior is increasingly difficult as more research on their abilities and preferences surfaces. Ross argues (2010) that improving captive animal care without an understanding of how animal minds work, or the scope in which they perceive and interact with their social and physical environments is not appropriate when deciding where and how these animals are going to live.

## **Conclusion**

This study presents results on how available space affects a group of captive chimpanzees living in a naturalistic enclosure. The chimpanzees show an increase in interindividual distance as space increases, and overall use more relative space when less space is available. Dyad differences highlight social affiliations and dominance

relationships in an environment where resource competition is low. It has previously been reported as a positive welfare aspect to give chimpanzees a choice in how and where to spend their time in captivity, this research adds to the literature by looking at how the group composition adjusts based on relative space.

Research has shown that in order for naturalistic enclosures to have a positive impact on both the animals housed inside and the public viewing them, they need to be complex and mentally stimulating allowing animals to make species-typical choices. Chimpanzee social relationships are an important aspect of their welfare, and allowing them choose who to interact with along with choosing to inhabit certain areas allows them to make choices as they would during party formation seen in fission-fusion in the wild.

The findings in this study encourage a deeper exploration into how choice and space affect social relationships in captivity. Including behavioral observations across different access conditions would allow a more in depth look at how behavior changes based on social proximity and available space. Research in captivity is important to understand how to provide animals with the socially and mentally stimulating environments, ensuring long term welfare heads in a positive direction.

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## Appendix A

**Photo 1:** Shows indoor enclosure and sliding glass doors.





**Photo 2:** Shows platforms, deep mulch floor, and indoor climbing structures.



**Photo 3:** Shows outdoor terrain and sliding glass doors.



## Appendix B

Tables show dyads mean (m), coefficients from the lm test with locked in as a baseline, and results from Kruskal –Wallis post hoc test (True = distances significantly differ).

<b>Cashew/Nana</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	3.018	3.018	1 Door/2 Doors	FALSE
1 Door	4.0434	1.0253	1 Door/Locked in	TRUE
2 Door	4.107	1.089	1 Door/Locked Out	FALSE
Locked Out	5.6472	2.6291	2 Door/Locked In	TRUE
			2 Door/Locked Out	TRUE
			Locked In/Locked Out	TRUE

<b>Nana/Kathy</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	3.4973	3.4973	1 Door/2 Doors	TRUE
1 Door	5.6466	2.1493	1 Door/Locked in	TRUE
2 Door	6.8384	3.3411	1 Door/Locked Out	FALSE
Locked Out	6.6956	3.1983	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Cashew/Kathy</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	3.7789	3.7789	1 Door/2 Doors	FALSE
1 Door	5.5544	1.7755	1 Door/Locked in	TRUE
2 Door	6.5069	2.728	1 Door/Locked Out	FALSE
Locked Out	6.2732	2.4943	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Kathy/Chuckie</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	3.8311	3.8311	1 Door/2 Doors	FALSE
1 Door	4.6844	0.8533	1 Door/Locked in	TRUE
2 Door	5.2992	1.4681	1 Door/Locked Out	FALSE
Locked Out	6.1491	2.318	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Nana/Chuckie</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	4.6831	4.8631	1 Door/2 Doors	TRUE
1 Door	6.749	2.0718	1 Door/Locked in	TRUE
2 Door	8.4982	3.8151	1 Door/Locked Out	FALSE
Locked Out	7.711	3.0279	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Nana/Optimus</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	4.7727	4.7727	1 Door/2 Doors	TRUE
1 Door	6.9757	2.203	1 Door/Locked in	TRUE
2 Door	8.1673	3.3946	1 Door/Locked Out	FALSE
Locked Out	7.0574	2.2846	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Cashew/Chuckie</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	4.8262	4.8262	1 Door/2 Doors	TRUE
1 Door	1.969	1.969	1 Door/Locked in	TRUE
2 Door	3.4495	3.4495	1 Door/Locked Out	FALSE
Locked Out	3.3177	3.3177	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Kathy/Optimus</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	4.8706	4.8706	1 Door/2 Doors	FALSE
1 Door	7.2814	2.4108	1 Door/Locked in	TRUE
2 Door	8.0356	3.165	1 Door/Locked Out	FALSE
Locked Out	6.903	2.0324	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Cashew/Optimus</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	5.0267	5.0267	1 Door/2 Doors	FALSE
1 Door	7.2715	2.2447	1 Door/Locked in	TRUE
2 Door	8.1135	3.0868	1 Door/Locked Out	FALSE
Locked Out	7.8699	2.8432	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Hank/Optimus</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	5.2728	5.2728	1 Door/2 Doors	FALSE
1 Door	6.7549	1.482	1 Door/Locked in	TRUE
2 Door	7.5451	2.2723	1 Door/Locked Out	FALSE
Locked Out	7.7297	2.4569	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Chuckie/Optimus</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	5.298	5.298	1 Door/2 Doors	FALSE
1 Door	7.6993	2.4013	1 Door/Locked in	TRUE
2 Door	8.0913	2.7933	1 Door/Locked Out	FALSE
Locked Out	7.3861	2.0881	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Cashew/Hank</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	5.7275	5.7275	1 Door/2 Doors	FALSE
1 Door	6.9347	1.2072	1 Door/Locked in	TRUE
2 Door	8.0654	2.3379	1 Door/Locked Out	TRUE
Locked Out	8.8035	3.076	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

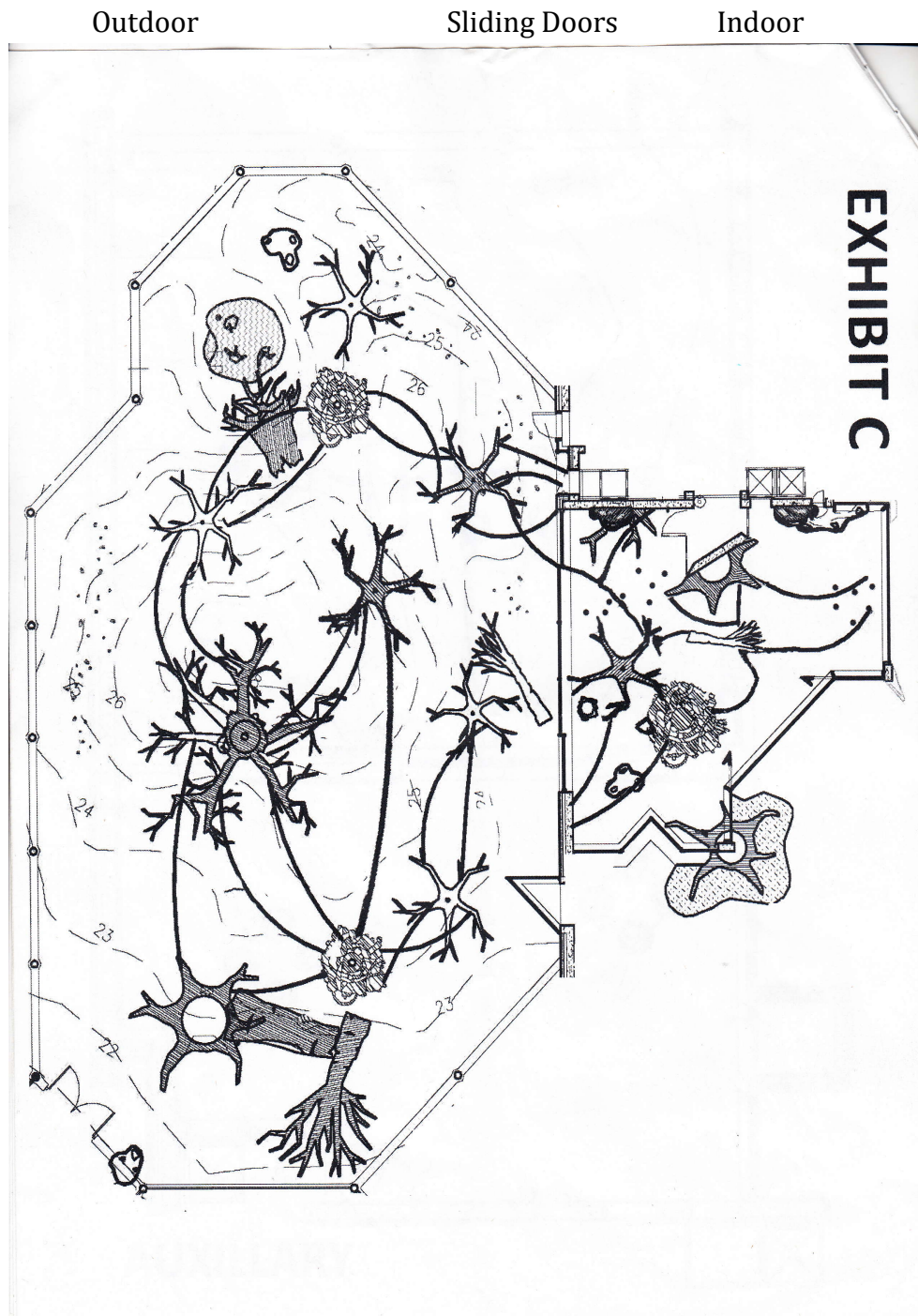
<b>Hank/Kathy</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	5.771	5.771	1 Door/2 Doors	FALSE
1 Door	6.9501	1.1791	1 Door/Locked in	TRUE
2 Door	7.9991	2.228	1 Door/Locked Out	FALSE
Locked Out	8.2096	2.4386	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Hank/Nana</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	5.7756	5.7756	1 Door/2 Doors	TRUE
1 Door	7.0829	1.3073	1 Door/Locked in	TRUE
2 Door	8.7068	2.9312	1 Door/Locked Out	FALSE
Locked Out	7.9838	2.2082	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

<b>Hank/Chuckie</b>				
Condition:	Means:	Coefficients:	Kruskal-Wallis (p=0.05):	
Locked In	6.2419	6.2419	1 Door/2 Doors	FALSE
1 Door	7.5444	1.3025	1 Door/Locked in	TRUE
2 Door	8.0569	1.8149	1 Door/Locked Out	FALSE
Locked Out	8.5564	2.3145	2 Door/Locked In	TRUE
			2 Door/Locked Out	FALSE
			Locked In/Locked Out	TRUE

## Appendix C

Birds-eye view of map of enclosure used to take data on electronic tablet.





Appendix D

Average Group Means by Dyad and Access

