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Comparison of Chimpanzee (*Pan Troglodytes*) Behavior on Tour and Non-Tour Days at Chimpanzee Sanctuary Northwest

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COMPARISON OF CHIMPANZEE (*PAN TROGLODYTES*) BEHAVIOR ON TOUR
AND NON-TOUR DAYS AT CHIMPANZEE SANCTUARY NORTHWEST

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Presented to

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In Partial Fulfillment

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Primate Behavior and Ecology

by

Allison Ann Farley

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CENTRAL WASHINGTON UNIVERSITY

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ABSTRACT

COMPARISON OF CHIMPANZEE (*PAN TROGLODYTES*) BEHAVIOR ON TOUR AND NON-TOUR DAYS AT CHIMPANZEE SANCTUARY NORTHWEST

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Allison Ann Farley

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In this study, I investigated the potential effect of a visitor program on captive chimpanzees' (*Pan troglodytes*) behaviors at Chimpanzee Sanctuary Northwest (CSNW) in Cle Elum, Washington. I used focal animal sampling to score behaviors from an ethogram of affiliative, aggressive and abnormal chimpanzee behaviors, as well as foraging and vigilance. During each sample, I recorded the focal's location within the enclosure and whether he or she was situated in locations that would be in view of visitors (present or not). I analyzed 720 minutes of data from each of the seven CSNW chimpanzees. I tested the hypothesis that the chimpanzee's behaviors would be different on tour and non-tour days. I predicted that on tour days the chimpanzees would have shorter foraging durations and longer durations of vigilant, aggressive and abnormal behaviors. I predicted that tour days would show changes (increase or decrease) in durations of social behaviors such as affiliation and inter-chimpanzee proximity compared to non-tour days. I also hypothesized that location preference would differ on tour and non-tour days. I observed significant differences for durations of vigilant, affiliative, aggressive, and abnormal behaviors and inter-chimpanzee proximity (P values

<0.05). I found no significant differences for foraging durations (P values >0.05).

Generalizations cannot be made about the potential effects of the tours because each chimpanzee varied with respect to some behaviors on tour and non-tour days. My results will aid sanctuary staff in their decisions to halt, alter, or retain this visitor program. My data may also serve as a case study for other sanctuaries.

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CHAPTER I

INTRODUCTION

There has been an increasing demand for sanctuaries to care for chimpanzees (*Pan troglodytes*) since the National Institutes of Health (NIH) 2013 decision to retire several hundred chimpanzees from biomedical research facilities (Kranendonk & Schippers, 2014) and their recent all inclusive designation as an endangered species (Messenger, 2015). A sanctuary is “a facility whose primary purpose is to provide security and humane care for captive great apes for as long as necessary” (Beck, Walkup, Rodrigues, Unwin, & Stoinski, 2007, p. 5). Some sanctuaries include educational programs with visitation (Beck et al., 2007). In such facilities, ensuring the optimal well-being of the animals in their care is priority over entertainment and education of the public (Pruetz & McGrew, 2001).

Similar to zoo environments, a potential conflict exists, however, between the priorities of a sanctuary and the need for funding and educational outreach (Fernandez, Tamborski, Pickens, & Timberlake, 2009; Morgan & Tromborg, 2007). This ongoing conflict is perpetuated by the fact that while effective public education can increase conservation efforts and lead to greater empathy for the species (Hosey, 2005), it often requires close proximity to and visibility of the animals (Davey, 2005; Hosey, 2000). Close proximity and high visibility could induce stress, thereby affecting the behavior of the animals (Fernandez et al., 2009; Hosey, 2000). Stress and welfare are closely associated concepts (Barnard & Hurst, 1996), and should be defined from the individual’s perspective (Broom, 1986). Broom (1986) defines welfare as an individual’s “state as regards its attempts to cope with the environment” (p. 524). Behavioral modifications as

seen in coping mechanisms (Broom, 1991) are used to ameliorate stress. Inferences about the welfare state of an individual can be assessed through the presence of coping behaviors (Broom, 1986; Broom, 1991; Barnard and Hurst, 1996).

Welfare and coping are both on a spectrum (i.e., good to poor welfare and high to low energy output) (Broom, 1986). Welfare should be assessed in terms of what each species has evolved to cope with (Barnard & Hurst, 1996), and whether it is deemed successful or exhaustive (Broom, 1986). From these perspectives, if a captive setting creates an environment that does not allow for successful coping or coping mechanisms observed in the wild, the welfare of the captive individual can be potentially compromised.

The limitations imposed by the captive environment constrain an individual's opportunity to express the species' full behavioral repertoire (Sajjad, Farooq, Anwar, Khurshid, & Bukhar, 2011). The restrictions of captive settings include reduced space, predetermined social group composition, predictable and structured environments (Morgan & Tromborg, 2007; Pruett & McGrew, 2001; Wemelsfelder & Birke, 1997), lack of predation, and an overall lack of agency (Clark, 2011). For species such as the chimpanzee, these restrictions vary greatly from a wild, natural environment. In the wild, the average daily range of the chimpanzee vary from 500-1,000 meters, their daily nutrition is obtained through arboreal foraging excursions for herbaceous vegetation and fruit, and their community structure consists of a mixed-sex, fission-fusion pattern (Pruett & McGrew, 2001; Stumpf, 2011). In addition to limiting the behaviors observed in the wild, captivity induces stress due to circumstances that are not experienced in the

wild, for example, confinement and consistent proximity to, interaction with, and dependency on human care (Morgan & Tromborg, 2007).

The diverse spectrum of natural chimpanzee behavior, paired with an environment that presents stressors different from those experienced in the wild (Frankham et al., 1986), inhibits the ability of the individual to respond in species-typical ways, such as fleeing and physical defense (Crofoot, Lambert, Kays, & Wikelski, 2010; Davis, Schaffner, & Smith, 2005; Knight, 2009). The inability to fully express species-typical behaviors can lead to a reduction in well-being (Chelluri, Ross, & Wagner, 2013; Coe, Scott, & Lukas, 2009; Fouts, Fouts, & Waters, 2002; Hosey, 2005; Wells, 2005). The presence of novel stressors in captive environments inhibits the use of coping mechanisms observed in the wild (escape and defense) and can therefore affect an individual's welfare (Barnard & Hurst, 1996).

In an attempt to alleviate these consequences of captivity and stimulate species-typical behaviors, caregivers provide enrichment for primates (Birke, 2002; Carder & Semple, 2008; Clark, 2011; Mallapur, Anindya, & Waran, 2005; McPhee & Carlstead, 2010; Morgan & Tromborg, 2007; Pruetz & McGrew, 2001; Wood, 1998). The opportunity to exercise and stimulate cognitive and sensory capabilities is crucial to the animal's behavioral needs and well-being (Clark, 2011; Carder & Semple, 2008; Carlstead & Shepherdson, 2000; Fernandez et al., 2009; Hosey, 2000; Hosey, 2005; McGrew, 1981; Knight, 2009; Pruetz & McGrew, 2001; Wood, 1998).

There is a perpetual conundrum between key decisions made for the benefit of the individuals in captivity and decisions made for the benefit of the industry in order to improve educational outreach and increase financial support (Davey, 2005; Fernandez et

al., 2009; Hosey, 2000; Hosey, 2005; Keane & Marples, 2003; Mason, 2000). Although this dichotomy may seem irreconcilable, there are decisions that can be made that will benefit captive individuals and help meet educational and financial goals. In their research on how the public perceived animals in captivity, Reade and Waran (1996) found that educational exposure to animals in zoo environments led to both increased empathy for the animals and a greater understanding of conservation efforts. Awareness and empathy such as this, paired with financial gain through visitation and donations, could provide ultimate net benefits for the species being conserved. If implemented in a way that has a limited effect on behaviors indicating stress, visitation to captive settings, including sanctuaries could be highly beneficial.

Research on primates has found correlations between the human audience and frequencies of behavior that indicate stress (Birke, 2002; Blaney & Wells, 2004; Carder & Semple 2008; Chamove, Hosey, & Schaetzel, 1988; Clark et al., 2011; Davis et al., 2005; Glaston, Geilvoet-Soeteman, Hora-Peck, & van Hooff, 1984; Keane & Marples, 2003; Klailova, Hodgkinson, & Lee, 2010; Mallapur et al., 2005; Sherwen et al., 2015; Wells, 2005; Wood, 1998). Behavioral frequencies defined as indicative of stress include abnormal (Clubb & Mason, 2007), aggressive (Honest & Martin, 2006a), hypervigilance and inactivity (Birke, 2002), and changes in affiliation (Chamove et al., 1988; Cohen, Kaplan, Cunnick, Manuck, & Rabin, 1992). In order to maintain the welfare state of captive animals, management can ameliorate stress through mitigation. It can aid in minimizing the costs to the individuals being viewed, while simultaneously maximizing the net benefits of public funding and education. A regular assessment of behavior is a

critical aspect of maintaining the welfare of captive nonhuman primates (Birke, 2002; Wood, 1998).

Chimpanzee Sanctuary Northwest (CSNW), located in Cle Elum, Washington was established in 2003. It is home to seven chimpanzees released from biomedical research in 2008. The chimpanzees were used as breeders and for hepatitis research. A visitor program has occurred since summer 2013, but there is a lack of information on how visitors might be affecting the chimpanzees' welfare. Tours at CSNW differ from zoos in many aspects: they are led by a caregiver, do not allow visitors to freely move, and there is no close contact or interaction between the visitors and the chimpanzees. The educational portion of the tour prior to viewing the chimpanzees provides information on CSNW and encourages visitors to maintain a respectful demeanor. Throughout the tour, the ecology of chimpanzees, their past experiences, and respect for their well-being is communicated by the caregiver leading the tour. CSNW staff are considering an expansion and formalization of the visitor program and need information to assess potential costs and benefits. My study provides this information.

My study was conducted at CSNW using published ethograms of chimpanzee behavior. I hypothesized that the chimpanzees' behavior would be different on tour and non-tour days. I predicted the chimpanzees would engage in longer durations of vigilant, aggressive, and abnormal behaviors, shorter durations of foraging, and that frequencies of social behaviors such as affiliation and inter-individual proximity would change (increase or decrease) when visitors were present compared to baseline data collected for these variables when visitors were absent.

My study also included data collected from an optional survey CSNW offers visitors after the tour. The survey consists of fifteen questions that provide CSNW staff with basic information about the visitors' experience. I focused on four questions that specifically relate to education, empathy, and funding. I assessed the responses to determine whether the tours were contributing to the net benefits of tourism, as described by Fernandez et al. (2009). I hypothesized that survey data would show that tours contribute to increased knowledge of both chimpanzees and the passions and efforts behind CSNW, increased empathy for chimpanzees, and increased funding through donations.

CHAPTER II
LITERATURE REVIEW
Chimpanzee Species Profile

Distribution

Stumpf (2011) provides a species profile of humankind's closest living relative, the chimpanzee (*Pan troglodytes*). The chimpanzee is adapted to diverse range of habitats that span across equatorial Africa. Their distribution extends longitudinally across multiple ecosystems and reaches altitudes of up to 3,000 m. Community range size varies from 10 km² to 50 km² in the central chimpanzee (*Pan troglodytes troglodytes*) (Goodall, 1986) and 16-30 km² in the western chimpanzee (*Pan troglodytes verus*) and over 50 km² in the eastern chimpanzee (*Pan troglodytes schweinfurthii*) (Herbinger, Boesch, & Rothe, 2001). Regional, ecological variation selects for a diverse spectrum behavior with respect to territoriality, reproduction, community structure, hunting processes, food acquisition, and distribution and range between populations. Sleeping behaviors include nightly arboreal nests made from woven tree branches.

Diet

Based on local ecology, the chimpanzee diet varies in the distribution and availability of foods; chimpanzees rely on fruit everywhere (Stumpf, 2011). They also eat terrestrial herbaceous vegetation and animal protein. Food is acquired through foraging and hunting practices, the latter of which varies depending on canopy cover and foliage density.

Group Structure

Chimpanzees are a mobile, arboreal, and terrestrial species (Stumpf, 2011). They are very social and live in complex, hierarchical communities. Population sizes vary from a few individuals to over 100. Chimpanzee communities are fluid and highly interactive. Conflict is inherent to such social complexity, and aggression is a common behavior. Grooming is an example of a behavior that mitigates aggression. Conflict and resolution occur within and between communities. Chimpanzees are territorial with variability in intergroup proximity and range overlap between groups. Intercommunity hostility occurs in defense of territory, food, and females, and perimeter patrols occur monthly.

The chimpanzee community is multifemale/multimale, and group structure is influenced by fission fusion dynamics. Therefore, the grouping patterns vary between sites. Males are philopatric, and females emigrate from their natal communities after sexual maturation. Males form coalitions and exchange support in mate guarding, hunting, and intergroup aggression. Female relationships vary among subspecies depending on the ecological factors that determine access to food and mates. Affiliative behaviors such as grooming are prevalent. Social interactions are used to maintain social bonds and reconcile. An up-rank directionality of inter-individual interactions creates an altruistic exchange for which low-ranking individuals can maximize proximate social benefits by affiliating with high-ranking individuals (Newton-Fisher & Lee, 2011). Chimpanzee reproduction is defined by long interbirth intervals and high maternal investment. Mating dynamics and social strategies are used to maintain social organization, maximize access to food, and simultaneously minimize the costs of

complex dominant exchanges, such as injury and increased stress levels, which results in varying community structures.

In nature, chimpanzee cognition has been studied since Jane Goodall's research in Gombe began in the 1960s. Her observations of tool use altered perceptions of chimpanzee cognition. As decades have passed, studies have further provided evidence of complex cognitive abilities. Similar to regional variations in community structure, reproductive strategies, and diet, there is also diversity in tool use, which has led to years of study of culture in chimpanzees (Goodall, 1986).

Chimpanzees in the wild have multifaceted, diverse lives (Goodall, 1986). They rely on complex decision-making strategies and social cohesion. By contrast, the static structure of captive environments does not provide the wild's complexity (Mason et al., 2013; Wemelsfelder & Birke, 1997). Captive settings vary, and those that provide opportunities for cognitive enrichment and social interactions more closely mimic wild conditions (Clarke, Juno, & Maple, 1982; Pruett & McGrew, 2001). Due to the innate nature of certain chimpanzee behaviors, expressions of these behaviors are still observed in captivity despite the controlled static environment they reside in, indicating the importance of a full consideration of species-typical needs (Pruett & McGrew, 2001).

Captive Primates

The captive settings in which thousands of nonhuman primates reside vary in size, design, location and function. Modern zoological settings are grounded in education and entertainment for the public (Reade & Waran, 1996) and vary in enclosure design and provision of enrichment. Laboratory settings are designed for the purpose of biomedical

research on nonhuman primates to make advances in medicine (Rogers et al., 2006). In these controlled laboratory environments, individuals are restrained physically and may not be encouraged or able to participate in species-typical behaviors (Darken-Schultz, Pape, Annenbaum, Saltzman, & Abbott, 2004). Sanctuaries can provide “rich physical and social environments that allow individuals to recover from the stress they experienced in being removed from their mother and from life in the wild” (Farmer, 2002 as cited in Wobber & Hare, 2011, p. 1). Sanctuaries can also allow individuals to recover from the invasive research, deprivation, and trauma associated with biomedical facilities (Lopresti-Goodman, Kameka, & Dube, 2013). In contrast to zoological settings, public education, research, and tourism are secondary or absent for some sanctuaries (Farmer, 2002 as cited in, Beck, 2010; Pruett & McGrew, 2001).

Nonhuman primates have been housed and bred in captivity for centuries (Mason, 2000). The first recorded zoos date to the 15th century in Egypt (Alexander, 1979 as cited in Mason, 2000, p. 333; Davey, 2006). Zoological environments have had various purposes throughout history, beginning as a form of entertainment due to their spectacle nature (Rumbaugh, 1972). Their purpose evolved into an avenue for education, offering the public information on species diversity (Rumbaugh, 1972).

Individual nonhuman primates can live an entire life span in medical facilities. The estimated numbers in the U.S. total to 112,000 monkeys (The Humane Society of the United States, 2016) and 675 chimpanzees (Chimpcare, 2016) currently housed in biomedical laboratories. The eight National Primate Research Centers (NPRC) located in the U.S. house 28,000 individuals of 20 species of nonhuman primates used for biomedical research (NCRR, 2009).

The rhesus macaque (*Macaca mulatta*) (Rogers et al., 2006) and the chimpanzee (Olson & Varki, 2002) are the most widely used subjects, due to morphological, physiological, biological, and genetic similarities between their species and humans (NCRR, 2009; Quigley, 2007). The rhesus macaque is studied for a number of neurological, psychobiological, and physiological disorders and diseases (Rogers et al., 2006). The high percentage of DNA shared between humans and chimpanzees have made them biologically relevant subjects for medical research on hepatitis A, B, and C as well as the mapping of the human genome (Fouts et al., 2002; Olson & Varki, 2002; Quigley, 2007).

The social and legal movement for the retirement of nonhuman primates from biomedical research facilities has created a situation in which orphaned individuals are ill adapted for the wild due to differences in captive and wild settings and the physical and social deprivation associated with captivity (Frankham et al., 1986; McPhee & Carlstead, 2010; Wobber & Hare, 2011). As a result, chances for successful reintroduction to the wild are low (Frankham et al., 1986; Ha, Robinette, & Davis, 2000; McPhee & Carlstead, 2010). Retired primates are sometimes relocated to zoos and sanctuaries (Kranendonk & Schippers, 2014; Reimers, Schwarzenberger, & Preuschoft, 2007). Sanctuaries are designed to provide an enriching environment and promote species-typical behaviors, such as foraging and social interactions, that will aid in recovery by improving the mental and physical health of the nonhuman primates (Brune, Brune-Cohrs, McGrew, & Preuschoft, 2006; Kranendonk and Schippers 2014; Lopresti-Goodman et al., 2013; Pruett & McGrew, 2001).

Kranendonk and Schippers (2014) observed the behavior of six adult chimpanzees that were relocated from a laboratory setting to a Dutch sanctuary. The results of their study provide evidence for changes in behavior in the sanctuary compared to the laboratory. Acclimations to sanctuary life were inferred from increases in social affiliation and decreases in aggressive behaviors. This study demonstrates the potential for sanctuaries to influence nonhuman primate behavior in ways that are more reflective of a behavioral repertoire seen in wild populations, suggesting an active lifestyle in which the individuals have the opportunity to exercise their natural instinctual behaviors despite limitations imposed by living in captivity (Carlstead & Shepherdson, 2000; Pruett & McGrew, 2001).

Chimpanzee Behavior

Expressions of species-typical behaviors are a measure of well-being (Barnard & Hurst, 1996; Bloomsmith, Alford, & Maple, 1988; Chelluri et al., 2013; Coe et al., 2009; Dawkins, 2004; Fouts et al., 2002; Mason, 1991; McPhee & Carlstead, 2010; Pruett & McGrew, 2001; Wells, 2005). Based on correlations between an individual's welfare and expressions of his or her natural behavior, it is important to consider behaviors observed in the wild, which are constrained or impossible in captivity (Clubb & Mason, 2007; Mason, Clubb, Latham, & Vickery, 2007). In captivity, behaviors such as migration, foraging, and cognitive stimulation through complex decision making cannot be fully exercised due to the scheduled, controlled, and confined environment of captive settings (Carlstead & Shepherdson, 2000; Sajjad et al., 2011). A lack of such behavioral

opportunities has psychological, neurophysiological, and cognitive welfare implications (Fouts et al., 2002).

Studies on neurological mechanisms in the brain have shown that performance of species-typical behaviors produce physiological rewards. The stifling of these behaviors has welfare implications, causing the same neurological consequences of withdrawal from artificial drug use (Boissy et al., 2007). Chimpanzee-specific behaviors observed in wild populations occur within complex social and physical environments. Wild chimpanzee populations exhibit flexibility in complex social interactions and variable environmental conditions (Hosey, 2005; Khan, 2013; Stumpf, 2011). The wild environment encourages a spectrum of behaviors such as foraging, hunting, exploration, terrestrial and arboreal migrations, and the ability to socialize within dynamic, hierarchical relationships (Chelluri et al., 2013; Khan, 2013; McPhee & Carlstead, 2010; Pruett & McGrew, 2001; Stumpf, 2011). The threshold at which an individual can no longer express its species-typical behaviors efficiently to cope and mitigate stressful stimulants in the physical and social environment is a concern when assessing the welfare of captive individuals (Carlstead & Shepherdson, 2000; Carlstead, 1996 as cited in Sajjad, 2011; Dawkins, 2004; Morgan & Tromborg, 2007).

Definitions of Stress

Stressors are a key factor in animal well-being (Etim, Offiong, Eyoh, & Udo, 2013). In their discussion on published theories of stress and animal welfare, Barnard and Hurst (1996) describe stress as “environmental impositions, internal or external, that tax coping mechanisms” (p. 411), that reduce welfare. Etim et al. (2013) refer to a stressor as any external stimulus that challenges homeostasis within an individual. Stress can manifest through both physiological (e.g., cortisol levels) and behavioral (e.g., stereotypies) symptoms (Honest & Marin, 2006a). Due to the pervasive nature of stress, animals have evolved mechanisms to cope with and mitigate its negative effects (Trofimuiuk & Braszko, 2015). Observed frequencies of behaviors such as escape, defense, nourishment, aggression, affiliation, and stereotypies have been correlated with stress levels (Birke, 2002; Chamove et al., 1988; Chelluri et al., 2013; Davis et al., 2005; Duncan, Jones, von Lierop, & Pillay, 2013; Fernandez et al., 2009; Glaston et al., 1984; Goodall, 1986; Honest & Marin, 2006a; Hosey, 2000, Hosey, 2005; Maestriperi, 2010; Mallapur et al., 2005; Mason, 1991; McPhee & Carlstead, 2010; Mitchell et al., 1991; Quadros, Goulart, Passos, Vecci, & Young, 2014; Wells, 2005).

Depending on the behavioral resources available to an individual, stress can be alleviated socially or asocially through coping mechanisms, but the confined and controlled environment of captivity limits the strategies an individual can use to ameliorate the stressor (Carlstead & Shepherdson, 2000). As a result, the stressors induced by captivity, as well as human presence, must be considered and regularly assessed as a part of caregiving (AZA, 2010; Carlstead & Shepherdson, 2000; Hosey, 2005). To assess the potential causes of stress, researchers should compare the occurrence

of behaviors (indicative or non-indicative of stress) with the contextual circumstances of the environment (McPhee & Carlstead, 2010) (e.g., feeding, temperature, time of day, caregiver-animal interactions, and presence of visitors).

Chelluri et al. (2013) and Jensvold (2008) studied caregiver interactions and chimpanzee and gorilla (*Gorilla gorilla*) behavior, showing evidence for changes in behavior dependent on the type and frequency of interactions between the caregivers and apes. Chelluri et al. (2013) conclude that continued study of the consequences of interaction should be evaluated regularly due to the behavioral changes observed in the individuals even during those interactions assumed to be enriching.

Similarly, visitors also have the potential to induce stress and negatively affect animal welfare (AZA, 2010; Birke, 2002; Fernandez et al., 2009; Hosey, 2000; Wells, 2005). The mitigation of the effects of visitor presence has been studied for a variety of species and captive settings (Birke, 2002; Blaney & Wells, 2005; Chamove et al., 1988; Clark et al., 2011; Claxton, 2011; Clubb & Mason, 2007; Glaston et al., 1984; Hosey, 2000, Hosey, 2005; Mallapur et al., 2005; Sherwen et al., 2015; Stoinski, Jaicks, & Drayton, 2011; Wells, 2005; Wood, 1998). Researchers have provided solutions for resolving the sometimes conflicting goals of education, fund raising, and the protection and maintenance of welfare of the individuals in captivity (Fernandez et al., 2009; Hosey, 2005). Khan (2013) concluded that visitors should be provided with information and awareness about the animals in a way that does not impose stress on the animals, limiting potential welfare implications.

Some researchers have found evidence that human presence is a form of enrichment in which animals are positively stimulated by novel interactions (Claxton,

2011; Morris, 1964). Others have found that animals become habituated to and are no longer affected (positively or negatively) by the presence of humans (Hosey, 2000; Snyder, 1975). Some researchers have suggested that changes are not perceivable (McDougall, 2012), while others have found that behavioral changes were not significant (Stoinski et al., 2011). In contrast to these studies, many have found significant correlations between the presence of visitors and changes in the animals' behaviors that are indicative of a decrease in well-being (Birke, 2002; Blaney & Wells, 2005; Carder & Semple, 2008; Chamove et al., 1988; Clubb & Mason, 2007; Davis et al., 2005; Glaston et al., 1984; Hosey, 2008; Keane & Marples, 2003; Khan, 2013; Mallapur et al., 2005; Mitchell et al., 1991; Sherwen et al., 2015; Quadros et al., 2014; Wells, 2005; Wood, 1998).

Chimpanzee Behavioral Contexts

Ethograms of chimpanzee behavior have been created and used in captive behavioral research (Duncan et al., 2013; Lopresti-Goodman, et al., 2013; Jensvold, 2008; Mulcahy, 2001; Pederson, King, & Landau, 2005; Wells, 2005). Behavioral frequencies noted as indicative of stress include those within abnormal, aggressive, and affiliative contexts and are used to assess the welfare of captive nonhuman primates (Carder & Semple 2008; Hosey, 2005; Mason, 1991; McPhee & Carlstead, 2010; Wells, 2005). Studies on visitor effects have provided evidence of various correlations between these behavioral frequencies and stress (Birke, 2002; Bernstein & Gordon 1974; Blaney & Wells, 2005; Carder & Semple 2008; Chamove et al., 1988; Clark et al., 2011; Davis et al., 2005; Glaston et al., 1984; Hosey, 2000; Hosey, 2005; Keane & Marples, 2003;

Mason, 1991; Mallapur et al., Mitchell et al., 1991; Quadros et al., 2014; Sherwen et al., 2015; Wells, 2005; Wood, 1998).

I chose these behaviors because of their prevalence in previous research on the visitor effect and their implications with respect to stressful environments and reduced welfare (Hosey, 2000; Hosey, 2005). For example, my ethogram included behaviors such as groom (Jensvold, 2008; Jensvold, Buckner, & Stadtner, 2010), hit and threat (Mulcahy, 2001), and autogroom and self-scratch (Pederson et al., 2005). When rates of these behaviors increase or decrease from the individual's baseline behavior rates, I can infer that there is an increase in stress. Each of these three behavioral contexts, aggressive, affiliative, and abnormal, are considered in more detail below.

Aggressive Behaviors

Chimpanzee aggression is a behavioral response to community conflict (Duboscq, Agil, Engelhardt, & Thierry, 2014) and reflects the complexity of chimpanzee society (de Almeida, Ferrari, Parmigiani, & Miczek, 2005; Goodall, 1986; Honess & Marin, 2006b). Its multifunctional use in chimpanzee society results in its occurrence in many situations. Behaviors associated with aggression, e.g., bite, slap, charge, display, and threat (Mulcahy, 2001; Pederson et al., 2005), are costly to all members of the interaction (Duboscq et al., 2014). Physical costs include internal and external injury, as well as increased anxiety, heart rate and stress hormone levels (Arnold & Aurieli, 2006 as cited in Duboscq et al., 2014). Welfare implications must be considered when frequencies of aggression create an imbalance between the costs and benefits of the interactions. At low

rates, aggression will be less likely to cause anxiety and stress (Chelluri et al., 2013; Honess & Marin, 2006b).

Goodall (1986) assessed the function of aggressive behavior and noted the importance of considering the context in which it occurs. Assessing potential stressors in the environment, such as the presence of visitors, in relation to frequencies of aggression, suggests a potential role of stress in aggressive interactions and its function for relieving such stress. For example, in the wild, a relaxed chimpanzee is less likely to threaten a subordinate one during feeding (Goodall, 1986), suggesting the potential that stress can be a factor in the presence or absence of aggression. Individuals may engage in higher rates of aggression due to a state of stress. In their review on the function of aggression, Bernstein and Gordon (1974) noted that extreme aggression occurs in situations where the animal is unable to escape. The inability to escape or retreat from the stress induced by visitors in captive environments (Fernandez et al., 2009; Hosey, 2005) may increase stress levels, leading to intragroup aggressive interactions (Carlstead & Shepherdson, 2000). Including aggressive behaviors in my ethogram is relevant to my study because their frequencies on days with and without visitors can provide information on the chimpanzees' stress levels.

Abnormal Behaviors

Abnormal behaviors, also referred to as displacement behaviors and stereotypes, are expressions of internal conflicts within an animal (Troisi, 2002) and have been defined as repetitive, invariant, with no obvious goal or function and often occur as a result of problems that are unsolvable (Dawkins, 2004; Odberg, 1989). In nonhuman

primates in particular, abnormal behaviors (e.g., self-grooming, self-scratching) are defined as comfort behaviors (Troisi, 2002). Such comfort behaviors have been suggested to relieve anxiety due to past traumatic stress (Lopresti-Goodman et al., 2013) and chronic and acute stress (Chamove et al., 1988; Duncan et al., 2013; Hosey, 2005; Mason, 1991). Most studies on primates' abnormal behaviors focus on captive populations (Brune et al., 2006; Carder & Semple, 2008; Chamove et al., 1988; Clarke et al., 1982; Duncan et al., 2013; Khan, 2013; Lopresti-Goodman et al., 2013; Mason, 1991; Mallapur et al., 2005) with less information available on their presence in the wild (Brune et al., 2006). Abnormal behaviors vary between individuals (Mason, 1991) and include regurgitation, coprophagy, repetitive body movements, hair-pulling, self-slapping, spitting (Birkett & Newton-Fisher, 2011; Duncan et al., 2013; Honess & Marin, 2006a; Pederson et al., 2005), and repetitive self-grooming (Lopresti-Goodman et al., 2013). Evidence for their occurrence in stressful environments provide support for their coping and beneficial nature (Carder & Semple, 2008; Clubb & Mason, 2007; Duncan et al., 2013; Hosey, 2000, Hosey, 2005; Mason, 1991; Wells, 2005), further suggesting their reinforcing nature (Mason, 1991). As a result, rates of abnormal behaviors have been used as welfare indicators (Brune et al., 2006; Duncan et al., 2013; Mason, 1991; Swaisgood & Shepherdson, 2006), and it is important to consider the context and frequency of their performance (Broom, 1983; Duncan et al., 2013). When the rate creates an imbalance between the physical costs (e.g., harm or injury) and the benefits of their coping nature, abnormal behaviors are no longer considered beneficial, and the welfare of the individual is compromised (Duncan et al., 2013; Mason, 1991).

The neurological and physiological role of abnormal behaviors has been associated with the stimulation of the rewarding portions of the brain, ultimately subduing the stress-induced mechanisms of the body (Boissy et al., Brune et al., 2006). The challenge in diagnosing an abnormal behavior as one in response to a stressor, however, is due to the similarities in its performance with other behaviors within the animal's behavioral repertoire (Troisi, 2002). There are however, subtle differences in the performance of the behavior when comparing stressful and non-stressful environments (Brune et al., 2006; Troisi, 2002), for example, exaggerated movements or high repetition causing harmful consequences. Therefore, the context in which the behavior is expressed is crucial to decipher the behavior as abnormal. In identifying the behavior as abnormal, one can assess the environmental context and make decisions to eliminate potential stressors.

In a study on displacement behaviors in laboratory rats (*Rattus norvegicus*) Berridge, Mitton, Clark, and Roth (1999) considered the adaptive stress response of repetitive chewing, analyzing neurotransmission in stressful environments. Some rats were provided inanimate objects on which to orally fixate. The results showed evidence for "selective suppression of the stressor-induced increases" (Berridge et al., 1999, p. 193) in neurotransmission within the prefrontal cortical region of the brain. Neurological evidence such as this suggests the stress-response function of abnormal behaviors in promoting their rewarding expression in stressful environments, for example, where appropriate species-typical coping-mechanisms (e.g., escape) are not available.

Research on nonhuman primates also suggests that displacement activities are behavioral components of the adaptive stress response (Troisi, 2002). Chimpanzee coping

mechanisms, such as retreat or affiliation, are not always available in captivity. Captive environments that do not allow animals to engage in behaviors that provide relief from stressors, can lead to abnormal behaviors (Carlstead, 1996 as cited in Sajjad et al., 2011). From a social perspective, the absence of fission-fusion social formation and interaction in some captive settings results in the occurrence of abnormal behavior (Khan, 2013). A captive environment that lacks provisions of species-typical needs paired with no amelioration of stress can also lead to abnormal behaviors. Including abnormal behaviors in my ethogram is relevant to my study because their frequencies on days with and without visitors can provide information on the chimpanzees' stress levels.

Affiliative Behaviors

Prosocial, affiliative behaviors such as grooming (Jensvold, 2008; Jensvold et al., 2010) have been considered in many visitor effect studies (Chamove et al., 1988; Glaston et al., 1984; Hosey, 2008; Keane & Marples, 2003; Kuhar, 2008; Mallapur et al., 2005; Mitchell, et al., 1991; Quadros et al., 2014; Wood, 1998). Because both increases and decreases in affiliation are indicators of stress in captive environments (Hosey, 2005), this behavior has been difficult to apply as a general indicator of individual welfare. The suggestion that the welfare of an individual be assessed as a measure of the presence of species-typical behaviors has limitations particularly for affiliative behaviors. Measurements of affiliation should include the social and environmental context of the situation due to the consistent but diverse applications of affiliation within chimpanzee behavior. Comparing increases or decreases of affiliative frequencies across contextual environments, such as the presence or absence of visitors (Chamove et al., 1988), large or

small crowds (Birke, 2002; Chamove et al., 1988; Clark et al., 2011; Mitchell et al., 1991; Wood, 1998), or stable and unstable environments (Cohen et al., 1992), can provide information about welfare.

Individuals who are not apparently exposed to stressful situations are observed grooming one another, therefore suggesting that the presence of affiliation indicates the absence of stress and its use in maintaining individuals' social bonds and hierarchical status (Baker, 2004; Jensvold et al., 2010; Logan, Emery, & Clayton, 2012; Mallapur et al., 2005; Mitchell et al., 1991). In their study of zoo-housed gorillas, Coe et al. (2009) considered the presence of affiliative behaviors as a sign of an enriching enclosure encouraging species-typical behaviors, thus suggesting positive welfare states of the individuals.

By contrast, Cohen et al. (1992) compared the cellular immune response of long-tailed macaques (*Macaca fascicularis*) exposed to chronic stress in unstable environments to those in stable environments. Their results showed that individuals exposed to chronic stress had higher rates of affiliation and individuals who affiliated more showed an enhanced immune response. Individuals with low affiliation showed a suppression of immune response. Physiological evidence such as this supports hypotheses regarding the coping role of affiliation, and its potential welfare implications (Cohen et al., 1992; Sapolsky, 2005).

Chamove et al. (1988) considered the observed frequencies of affiliative behaviors in fifteen species of captive nonhuman primates. Their results were consistent with their interpretation of a stressful environment. The results of their studies across three different environmental contexts showed consistent decreases in affiliative

behaviors when comparing large versus small crowds, high and low visibility, and the presence versus absence of visitors. Evidence for decreases in affiliation in this study suggest potentially negative welfare states of the individuals. Both Cohen et al. (1992) and Chamove et al. (1988) show evidence for affiliation frequencies associated with the presence of stress in the environment, thus reinforcing the need for a contextual estimate of the associated environmental factors (McPhee & Carlstead, 2010).

Due to the varying frequencies of affiliation in studies that assess stressful environments, affiliative behaviors must be applied comparatively. Studies that compare affiliation frequencies rather than make assumptions based on the sheer presence of the behaviors as an indicator of stress, will provide more accurate information for welfare estimates. Proximity can also be seen as a form of social behavior, providing evidence for the maintenance of social relationships (Feldman, 2012; Fraser, Schino, & Aureli, 2008). The ability to maintain social relationships can improve well-being (Clark, 2011). Proximity as defined by multiple studies sometimes includes contact. For the purpose of my study I will separate proximity from affiliation based on contact (i.e., affiliation includes contact, proximity does not). Including affiliative behaviors in my ethogram and time spent in proximity is relevant because their frequencies on days with and without visitors can provide information about the chimpanzees' stress levels.

Visitor Effects

Human presence is a condition of captivity from which there is no escape and can be a consistent stressor (Birke, 2002; Fernandez et al., 2009; Hosey, 2000; Morgan & Tromborg, 2007; Quadros et al., 2014; Wells, 2005). In some captive environments (e.g.,

zoos), human presence includes both caregivers and an audience. The human audience is comprised of factors such as noise, size, activity, and proximity that “fluidly interact and mutually influence one another” (Wood, 1998, p. 228). These factors create a variety of captive contexts that can affect animal behavior (Hosey, 2000; Stoinski et al., 2011; Wood, 1998). The impact of the human audience on behavior is unique to the circumstances of each environment (Stoinski et al., 2011). Therefore, the welfare implications of the captive environment should be estimated by considering the factors of the human audience (Clubb & Mason, 2007; Fernandez et al., 2009; Hosey, 2005; Morgan & Tromborg, 2007; Stoinski et al., 2011) and how the enclosure allows for the animals to cope in species-typical ways (Birke, 2002; Carder & Semple, 2008; Chamove et al., 1988; Clubb & Mason, 2007; Coe et al., 2009; Fernandez et al., 2009; Kuhar, 2008; Mallapur et al., 2005; Morgan & Tromborg, 2007; Stoinski et al., 2011). The welfare of the captive individual is affected by both the behavior of the visitors and the animals’ ability to cope with those behaviors. Using a framework that considers the variability of captive environments (Fernandez et al., 2009; Stoinski et al., 2011), one can estimate the impact of the human audience on the animal’s stress level and well-being.

There is a perpetual conflict in the observation of captive animals (Fernandez et al., 2009; Hosey, 2005; Keane & Marples, 2003). This unavoidable challenge exists between the desires of the visitors to see the animal and the needs and well-being of the animals in captivity (Morgan & Tromborg, 2007). This conflict creates a situation in which the decisions made have the potential to inhibit critical factors necessary for the success of the industry (Fernandez et al., 2009; Morgan & Tromborg, 2007). Fernandez et al. (2009) presented the feedback loop: decisions made solely for the animals’ welfare

have the potential to inhibit the experience of the visitors, thus leading to negative views of the zoo environment and decreasing financial gain from the visitors. Financial gain is necessary for the maintenance of the zoo environment and conservation efforts (Fernandez et al., 2009; Hosey, 2005).

Creating an optimal balance (Morgan & Tromborg, 2007) between the animals' welfare and the visitors' experience is key for a successful tourism industry. Complex enclosures that encourage species-typical behaviors will improve the well-being of the animals (McGrew, 1981), and offer naturalistic experiences for the visitors increasing the educational appeal, thus creating a stimulating experience for the visitors (Fernandez et al., 2009; Hosey, 2005).

Visitor Presence

The majority of studies on zoo-housed primates indicate that visitors are stressful (Birke, 2002; Blaney & Wells, 2004; Carder & Semple, 2008; Chamove et al., 1988; Fernandez et al., 2009; Glaston et al., 1984; Hosey, 2000; Hosey, 2005; Keane & Marples, 2003; Khan, 2013; Lambeth, Bloomsmith, & Alford, 1997; Mallapur et al., 2005; Morgan & Tromborg, 2007; Quadros et al., 2014; Sherwen et al., 2015; Stoinski et al., 2011; Wells, 2005; Wood, 1998). Factors collectively associated with the human audience (i.e., size, noise, distance, activities, and the visibility of both the animal and visitor) influence how stressful visitors are. For example, animals may respond to quiet, small crowds, who are not significantly within the animals' visual field with no apparent ill-effect. Conversely, animals may respond to crowds that are large, loud, and highly visible with behaviors such as intergroup aggression, decreased foraging and changes in

affiliative behaviors (Birke, 2002; Chamove et al., 1988; Glaston et al., 1984; Kuhar, 2008; Mallapur et al., 2005; Wood, 1998).

Each factor can be studied separately, or the entirety of the human audience can be considered with animal behaviors compared on days with and without visitors (Chamove et al., 1988; Mallapur et al., 2005; Wood, 1998). In their studies of zoo-housed primates, both Chamove et al. (1988) and Wood (1998) observed captive animals' behavioral changes in the presence of visitors, such as decreases in foraging and affiliation and increases in aggression. In their study of captive macaques (*Macaca silenus*), Mallapur et al. (2005) observed behavioral changes in the presence of visitors, such as increases in aggression and abnormal behaviors. Comparing behaviors on days with and without visitors provides a foundation for assessing the overall impact of the human audience. Extrapolating from this broad perspective can provide a framework for further research.

Noise

The noise level of the human audience affects captive primates causing stress behaviors including increases in aggression, abnormal behaviors, and arousal as well as decreases in social behavior (Birke, 2002; Fernandez et al., 2009; Quadros et al., 2014). In their review of captive mammals, Fernandez et al. (2009) states that most primates reacted aversely to large, noisy groups. Noise is not a stimulus that is easily escapable (Quadros et al., 2014). In a study on zoo-housed orangutans (*Pongo pygmaeus*), Birke (2002) compared noisy versus quiet visitors and showed that increased noise, which is associated with larger group size, caused changes in orangutan behavior. Orangutans

exposed to large and loud crowds were more inactive which has been associated with reduced physical health. In a similar study, Quadros et al. (2014) found that zoo-housed primates showed increases in aggression when visitors were loud. Keane and Marples (2003) noted the association between crowd size and noise level (measured using a sound meter) in their study of captive zoo-housed gorillas, showing increases in aggression and decreases in affiliation when crowds were noisy.

Zoo-housed primates may not habituate to the varying octaves and levels of noises emitted by visitors and find it distracting and aversive (Birke, 2002; Quadros et al., 2014), thereby impacting their welfare. Quadros et al. (2014) recommended adding sound barriers to enclosures and providing opportunities for animals to retreat from high volumes.

Active Audience

An active audience is defined as one in which at least one visitor attempts to interact with the animals (Cook and Hosey, 1995; Hosey, 2005). Lambeth et al. (1997) researched archival databases of wounding and aggression in captive chimpanzees and found high rates of aggression and wounding on days of the week associated with high visitor activity and high rates of attempted interaction. Lahm (1981, as cited in Chamove et al., 1988) found less affiliative behavior in six species of nonhuman primates when visitors actively harassed the captive animals. Fernandez et al. (2009) in their review on the detrimental impacts on primate welfare noted that when rates of provocation by visitors were high, primates engaged in high rates of both intragroup and visitor-directed aggression, as well as abnormal behavior when visitors were more active. Birke (2002)

found that the tendency of the active audience to stare in an attempt to gain attention of captive orangutans might have increased the rate at which orangutans placed sacks over their heads.

Visibility and Distance

Forced proximity between animals and humans can be deleterious to animal well-being (Fernandez et al., 2009; Hosey, 2000; Morgan & Tromborg, 2007; Stoinski et al., 2011). Forced proximity and the lack of control over the amount of space between the animals and visitors play roles in the stress induced by the human audience (Fernandez et al., 2009; Glaston et al., 1984; Morgan & Tromborg, 2007; Stoinski et al., 2011). The perception of the visitors as an encroaching threat and the inability to escape by fleeing, a coping mechanism in the wild (Bernstein & Gordon, 1974; Crofoot et al., 2010; Knight, 2009; McDougall, 2012; Morgan & Tromborg, 2007), creates an unrelievedly stressful situation for the animal. In their study on visitor effects in zoo-housed gorillas, Stoinski et al. (2011) observed behaviors indicative of stress, such as displacement behaviors, in two family groups when the individuals were on exhibit in close proximity to the visitors in the glass viewing section. The authors suggested that elements of visitor proximity are relevant to gorilla behavior, noting that gorillas in exhibits that had retreat space did not show the same behavioral changes even in the presence of large crowds.

The visibility of the human audience also affects the behavior of primates in both the wild (Klailova et al., 2010; Knight, 2009; McDougall, 2012) and captivity (Blaney & Wells, 2004; Chamove, et al., Clark et al., 2011; 1988). Visibility is a multifaceted term when referring to visitor effects. Visibility can refer to how much the animals can see the

visitors, for example, if the visitors are wholly visible to the animals or appear larger than the animals. It can also refer to how much the animal is seen by the visitors, for example, whether an enclosure provides structures, vegetation, or retreat space for the animals to become less visible to the visitors. The threatening nature of the audience is influenced by the visitor visibility perceived by the animals as well as the relative angles between the visitors and animals. Chamove et al. (1988) conducted a study on the effects of the apparent size and visibility of the visitors. The researchers compared behaviors expressed by the primates when groups were crouched versus standing. Increases in aggression and abnormal behaviors as well as increases in activity were associated with a standing, highly visible audience. Behavioral changes decreased by half, when crowds crouched. Blaney and Wells (2004) discuss the effects of camouflage netting between zoo-housed gorillas and visitors, showing decreases in aggression and abnormal behaviors when netting was used.

Visitors may never truly become a neutral presence (Hosey & Druck, 1987; McDougall, 2012) and decreases in behaviors indicative of stress have been observed when the human audience was not entirely visible to the primates being viewed (Blaney & Wells, 2004; Chamove et al., 1988; Clark et al., 2011; McDougall, 2012). McDougall (2012) suggests that the location of the visitors and their visibility impact primate behavior, showing decreases in abnormal behaviors when humans were undetectable. His results suggest that for visitors to remain undetectable to the animals, they must maintain their distance and stay behind vegetation. The results from these studies provide support for the importance of limiting visitor visibility in zoo environments.

Audience Size

Audience size also influences the behavior of captive individuals (Birke, 2002; Chamove et al., 1988; Clark et al., 2011; Cook & Hosey, 1987; Kuhar, 2008; Lambeth, et al., 1997; Mitchell et al., 1991, Mitchell et al., 1992; Wood, 1998), and primates respond adversely to large groups of unfamiliar humans (Stoinski et al., 2011). The size of the visitor group can also be positively correlated to increases in visitor noise and staring behaviors (Keane & Marples, 2003). When audiences are large, captive primates show increases in aggression and decreases in social and affiliative behaviors (Birke, 2002; Chamove et al., 1988; Keane & Marples, 2003; Kuhar, 2008; Lambeth et al., 1997; Mitchell et al., 1991; Wells, 2005; Wood, 1998). Such behavioral changes raise concern for animal welfare (Birke, 2002; Fernandez et al., 2009; Hosey, 2000; Hosey, 2005; Hosey, 2008; Morgan & Tromborg, 2007).

Kuhar (2008) observed changes in captive gorilla behavior in response to visitor group size, where the gorillas retreated to less visible locations in the enclosure on days with high visitor numbers. Birke (2002) found similar results for captive orangutans showing that orangutans used sacks more frequently with high visitor numbers, which might be associated with stress avoidance. Wood (1998) studied the correlation between enrichment and high visitor numbers in captive chimpanzees and found an effect on the chimpanzees' interest in old and new enrichment: the enrichment did not offer the distraction that the authors' hypothesized at the beginning of the study. Morgan and Tromborg (2007) note that changes in activity budget, such as decreased foraging and affiliation due to the presence of large crowds, has welfare implications for animals.

Activity Budget and Mental Stimulation

A recognized goal of captive management is to ensure that the activity budget of captive individuals approximates that of their wild counterparts (Yamanashi & Hayashi, 2011; Pruetz & McGrew, 2001; Wemelsfelder & Birke, 1997). Welfare concerns could be raised if the presence of visitors causes the animals to retreat at rates that cause changes in activity budget and mental stimulation (Birke, 2002; Wood, 1998). Pruetz and McGrew (2001) consider the promotion of species-typical behaviors a top priority for humane captive chimpanzee care and encourage the creation of environments that offer mental and sensory stimulation. The elicitation of species-typical behaviors can be encouraged through enrichment and enclosure design (Clark, 2011; Clarke, Juno, & Maple, 1982; Coe et al., 2009; McPhee & Carlstead, 2010; Honess & Marin, 2006b). A large portion of the daily energy budget involves searching for food and the constant visual assessment of the surrounding environment (Treves & Pizzagalli, 2002). Novelty in a static environment can offer opportunities to perform species-typical behaviors such as foraging and vigilance (Clark, 2011; Pruetz & McGrew, 2001; Wemelsfelder & Birke, 1997). Mental stimulation can be enriching, in that it provides challenges that are typical in the wild (Clark, 2011; Clark et al., 2011; Pruetz & McGrew, 2001; Wemelsfelder & Birke, 1997). If visitor presence causes changes in the frequencies of such behaviors that potentially indicate stress, the dynamics of the visitor groups may require mitigation.

Enclosures that provide retreat space for the animals may not fully ameliorate visitor effect. For example, if the behavior of the visitors is such that the animal spends a large percentage of its daily activity budget inactive or in retreat rather than socializing, inspecting, foraging, and/or moving, the welfare of the individual may be compromised.

Studies have shown decreases in activity levels and time spent foraging when zoo visitors are present (Birke, 2002; Clark et al., 2011; Keane & Marples, 2003; Morgan & Tromborg, 2007; Wood, 1998).

Inactivity can indicate reduced health (Birke, 2002) because the animals are not exploiting the available environment (Claxton, 2011; Yamanshi & Hayashi, 2011). Enriching locomotor activities, such as foraging, are important to the concept of well-being due to their recognized function as instinctual, desirable behaviors (Dawkins, 2004; McPhee & Carlstead, 2010; Pruetz & McGrew, 2001). Mental and sensory stimulation is also important for health and can enrich an individual by encouraging behaviors in response to novelty in a captive environment such as vigilance and inspection of the environment (Claxton, 2011; Swaisgood & Shepherdson, 2005).

The location of the individual within the enclosure paired with the behaviors exhibited in that location could have important welfare implications (Clark et al., 2011). Mitigating measures may include supplying enrichment and foraging opportunities out of view of visitors. Including foraging and vigilance in my ethogram is relevant because durations on days with and without visitors can provide information on potential stress levels in the environment (Clark et al., 2011). If the chimpanzees are in retreat and not foraging on days with tours, energy budget will be a concern. Durations of vigilance can potentially indicate whether tours are a source of stress or enriching for the chimpanzees (Clark et al., 2011; Claxton, 2011).

Mitigation of Visitor Effects

Balancing the expectations of the visitors and the health and well-being of the animals is a key aspect in maintaining the benefits of tourism to captive environments. An optimal balance can be achieved by considering the contextual framework of the human audience and mitigating the particular circumstances unique to each captive site and each group of visitors. The majority of studies on visitor effects have concluded with suggestions for mitigating variables of the captive environment to maintain the welfare of the animals while simultaneously maintaining an enjoyable, educational experience for visitors (Birke, 2002; Blaney & Wells, 2004; Chamove et al., 1988; Clubb & Mason, 2007; Glaston et al., 1984; Mallapur et al., 2005; Sherwen et al., 2015; Wells, 2005; Wood, 1998).

Mitigation Through Enclosure Design

By understanding the full scope of the species' needs, the captive enclosure can provide the necessary resources for the species to thrive and cope in species-typical ways. For example, Carder and Semple (2008) and Wood (1998) highlighted the importance of daily enrichment to reduce the overwhelming presence of the human audience. Enrichment provided in particular areas of the enclosure could improve the welfare of the individuals while mediating stressors associated with visitors (Carder & Semple, 2008).

Enclosure design can also mitigate visitor effect by altering visitor visibility and distance. For example, orangutans find direct gaze from visitors threatening (Birke, 2002). Therefore, managers can design an enclosure that will keep the visitors and animals at particular angles to reduce the impact of human gaze. Birke (2002) suggested

enclosure designs that prohibit visitors from collecting in large groups. Chamove et al. (1998) also discussed the variable stress induced by the relative positions between the visitors and animals, suggesting that modifications to walkways and viewing locations can alter the perceived height and visibility of the visitors relative to the animals on exhibit. Lowering walkways and taller cages will make the visitors appear smaller. One-way viewing glass will greatly lower visibility of the visitors. The introduction of vegetation and camouflage could also reduce the visibility of the visitors and provide a more natural habitat (AZA, 2010; Blaney & Wells, 2004; Stoinski et al., 2011). Quadros et al. (2014) suggested the installation of auditory barriers to reduce the stress induced by constant noise. Keane and Marples (2003) noted a decrease in avoidance behavior by zoo-housed gorillas when a barrier separated the gorillas from visitors.

The animals' ability to retreat and escape from large, noisy, or active audiences is another important feature of enclosure design (Birke, 2002; Chamove et al., 1988; Duncan et al., 2013; Fernandez et al., 2009; Quadros et al., 2014; Stoinski et al., 2011). Many zoo enclosures are built to maximize the visibility of the animals, leading to forced proximity and potentially unwanted attention from the audience (Birke, 2002). Altering aspects of the enclosure design can mitigate this forced proximity. For example, Stoinski et al. (2011) suggest the topography of the enclosure, which offers a broad view of the environment, may prevent gorilla's from being surrounded by guests. This feature may have aided in the decreases in abnormal and aggressive behaviors for some gorillas.

Mitigation Through Management-Enforced Audience Conduct

Mitigation measures that reduce the stress induced by the captive zoo environment can also be applied beyond the perimeter of the enclosure. Keane and Marples (2003) recommend that park staff control audience behavior by enforcing conduct rules. Managers can set noise standards (Birke, 2002), crowd size limits (Fernandez et al., 2009), and prohibit interactions between visitors and animals (Keane & Marples, 2003). By thoroughly informing the visitors of the species' ecology and the effects of visitors' behavior on animals, managers can encourage respect for animals and enforce rules that will benefit the animals (Birke, 2002; Chamove et al., 1988; Fernandez et al., 2009; Keane & Marples, 2003; Quadros et al., 2014). For example, Birke (2002) discussed the importance of informing visitors about the threatening nature of human gaze, suggesting side-glances instead of direct gazes at orangutans. Management can also set maximum capacities for audiences throughout the day (Birke, 2002; Chamove et al., 1988; Glaston, et al., 1984; Mallapur et al., 2005; Morgan & Tromborg, 2007). These decisions will ultimately improve conditions for the animals and may improve the visitor experience.

Visitor Benefits

Benefits of visitor tourism start with educational materials intended to increase empathy and improve attitudes toward animal welfare and conservation (Morgan & Tromborg, 2007; Mason, 2000). Ensuring the expression of behaviors observed in the wild by providing an environment designed for species-typical needs will not only benefit the animals, but also provide positive, enjoyable and informative experiences for the

visitors, potentially increasing funding (Fernandez et al., 2009; Hosey, 2005; McPhee & Carlstead, 2010). In turn, this funding will not only ensure the quality and support of the captive setting but could also improve global conservation efforts, thus contributing to species' preservation (Fernandez et al., 2009; McPhee & Carlstead, 2010; Morgan & Tromborg, 2007; Wood, 1998). Studies have also suggested that zoo tourism, if implemented optimally, can even provide a form of enrichment for the animals (Clark et al., 2011; Claxton, 2011; Hosey, 2000; Morgan & Tromborg, 2007, Morris, 1964).

Relevance of Literature to My Study

I applied my knowledge of nonhuman primate behavior with respect to visitor presence and absence to my study of seven chimpanzees at CSNW. I collected data throughout the months scheduled for tours, on days with and without visitors. I quantified the chimpanzees' vigilant, aggressive, affiliative, abnormal, and foraging behaviors in order to assess durations indicative of stress. I quantified inter-individual proximity to assess social relationships. I quantified the chimpanzees' use of space. I hypothesized that the chimpanzees' behaviors would be different on tour and non-tour days. I predicted that on tour days, the chimpanzees would have shorter foraging durations, longer vigilance durations, and increased aggressive and abnormal behaviors. I predicted that affiliation frequencies and inter-chimpanzee proximity would change (increase or decrease) when compared on tour and non-tour days. I hypothesized that chimpanzees' use of space would differ on tour and non-tour days. I predicted that on tour days, durations of time spent indoors would be longer and durations of time spent outdoors would be shorter.

Finally, I analyzed data collected from visitor surveys to assess the potential benefits of the tours. The four survey questions analyzed were directly related to the potential benefits of visitor tourism to captive environments: education, empathy, and funding (Fernandez et al., 2009). I hypothesized that the surveys would provide evidence that tours benefit both CSNW and the public. I predicted an increase in public education of chimpanzee welfare and the purpose of sanctuaries, an increase in empathy towards wild and captive chimpanzees, and an increase in funding from the visitor donations.

The chimpanzees' behavioral frequencies were paired with the associated welfare implications noted in previous research, and the results were then weighed in comparison to the potential long-term benefits of the tour program, inferred from the survey data. The potential stress induced by the tours can be mitigated to maintain the ultimate benefits of the visitor tours while simultaneously minimizing the costs to the chimpanzees. Using this behavioral and survey data, CSNW can make a comprehensive assessment of the ultimate costs and benefits of the summer tours.

CHAPTER III

METHODS

My study was conducted at Chimpanzee Sanctuary Northwest (CSNW) in Cle Elum, Washington. The subjects included seven adult chimpanzees (six females ranging 39-43 years of age and one 33-year-old male). The chimpanzees have been housed together at CSNW since their 2008 retirement from biomedical research.

CSNW is located on a 10.5 ha farm. The co-directors live on the property. The enclosure contains four sections: playroom (111 m²), front room (26 m²), greenhouse (56 m²), and Young's Hill (~1 ha with an electric fence perimeter). The entire enclosure is equipped with enriching structures and materials to stimulate and encourage species-typical behaviors. The enclosure sections are connected allowing the chimpanzees access to both indoor and outdoor sections. Feeding is scheduled (breakfast: 1000, lunch: 1300, dinner: 1630) with minor variations due to weather and chimpanzee behavior. The chimpanzees are consistently exposed to familiar staff and volunteer caregivers.

Caregivers and staff arrive at ~0830, and cleaning begins at ~0900. Chimpanzees are free to move among the enclosure sections where humans are absent. Human staff never physically move the chimpanzees, and humans and chimpanzees never share the same space. When the cleaning procedures are complete, the chimpanzees have full access to all four portions of the sanctuary until after dinner, which is served at approximately 1600. Young's Hill is closed 1630-1700. At approximately 1700, the lead caregiver prepares the indoor enclosure for the night.

My research occurred in the 2 month period during which tours were scheduled (July 3rd-September 14th). The guests comprising the tour group were unfamiliar to the

chimpanzees, hence the concern that their presence might negatively impact the apes. I collected data for a total of 42 days (24 with tours, 18 without) to compare behaviors when visitors were present and when visitors were absent. Each data collection period was performed consistently during the hours scheduled for tours with an additional 30 minutes of observation pre- and post-tours (1200-1436) to control for variation in behaviors based on variable natural activity levels and exposure to extraneous environmental events (feeding and cleaning).

Using an ethogram adapted from multiple published studies (Table 1), I performed 10 minute continuous focal animal samples (Altmann, 1974) for each chimpanzee with a 2 minute rest between samples. I used two randomized sampling schedules per weekend (Friday-Saturday and Sunday-Monday) to compare individuals' behaviors at the same time on tour and non-tour days. I collected 14 focal samples per day. For each chimpanzee, I continuously recorded all observed behaviors during the 10 minute sample. I observed and recorded 36 behaviors; 21 were analyzed for the purpose of my study. Of the behaviors that were analyzed, 19 were categorized within three behavioral contexts: affiliative (Jensvold et al., 2010), aggressive (Mulcahy, 2001), and abnormal (Pederson et al., 2005). Two behaviors were not categorized within these contexts but considered for analysis due to similar welfare implications: vigilance (Clark et al., 2011; Treves, 2000; Pruett & McGrew, 2001) and foraging (Clark et al., 2011; Ross et al., 2011; Pruett & McGrew, 2001). A total of 15 recorded behaviors were not used for analysis and identified as other.

Table 1 Ethogram of chimpanzee behaviors observed, recorded, and analyzed and their behavioral contexts.

Behavior	Description	Behavioral Context
Hit	Strikes another individual, an object, or part of the cage with the hand, foot or other object (CHCI)	Aggressive (AG)
Bipedal Swagger	An upright or semi-upright posture, swaying from one foot to another (CHCI)	Aggressive (AG)
Charge	Quadrupedal locomotion with limbs moving fast and brought higher off the ground, head tucked far down into shoulders, angle of back horizontal, slapping sound usually pilo-erect hair (CHCI)	Aggressive (AG)
Display/Threat	Aggressive behavior without any clear and identifiable recipient. May include pilo-erection, and such behaviors as beating on or moving inanimate objects, stomping, slapping, swaying, hooting, chest-beat, or running. If these behaviors are directed towards an individual, score as non-contact aggression (NC). (AZA, 2010)	Aggressive (AG)
High Intensity Agonism	The focal chimpanzee engages in aggressive behaviors on this ethogram that are not mutually exclusive (Lilienfeld et al., 1999)	Aggressive (AG)
Threat Bark	Loud, sharp sounds usually given in long sequences with much variation in pitch; functions to protest another individual of the same or different species (Goodall, 1986)	Aggressive (AG)
Reassurance	An interaction in which one individual calms another after a high arousal situation. Behaviors include hug, kiss, hand hold, whimpering and crouching. The focal chimpanzee may be either delivering or receiving those behaviors (Jensvold et al., 2010)	Affiliative (AF)
Allogroom	A variety of skin care patterns directed at or received from other individual including hair parting with lips or fingers or objects; lip smacking and tooth clacking (Mulcahy, 2001)	Affiliative (AF)
Embrace	Gentle contact to another individual using the arms or another body part (Parr, Cohen, & de Waal, 2005)	Affiliative (AF)

Table 1 (continued)

Behavior	Description	Behavioral Context
Play	Interactions are marked by specific behaviors such as play face, laugh, play walk, tickling, or chasing. Behaviors include object play, head butts, dragging, or pinching. The play face and exaggerated behaviors are key indicators of this category. The focal chimpanzee may be either delivering or receiving these behaviors. (Jensvold et al., 2010)	Affiliative (AF)
Autogroom	Repetitive, self-directed exploration of chimpanzees' own fur (Pederson et al., 2005)	Abnormal (AB)
Self-Scratch	Repetitive, self-absorbed drawing of nails firmly across individuals' own body (Pederson, King, & Landau, 2005)	Abnormal (AB)
Pace	Locomote, usually quadrupedally, on substrate, covering and then re-covering route in stylized fashion with no clear objective (Khan, 2013)	Abnormal (AB)
Rock	Sway repetitively rhythmically, without piloerection. Usually side to side movement, but may be forward and backward or full circular motion of torso. Usually whole body, sometimes just the head. (Birkett & Newton-Fisher, 2011)	Abnormal (AB)
Yawn	The mouth opens widely, roundly and fairly slowly, closing more swiftly. Mouth movement is accompanied by a deep breath and often closing of the eyes and lowering of the brows (Troisi, 2002)	Abnormal (AB)
Coprophagy	Deliberate ingestion of feces (AZA, 2010)	Abnormal (AB)
Urophagy	Deliberate ingestion of urine. Can be from themselves or another individual (AZA, 2000)	Abnormal (AB)
Lip Flip	The upper lip is rolled up and back towards the nose (Goodall, 1989)	Abnormal (AB)
Foot Tap	Fast pace, repetitive movement of the heel up and down in a non-play context	Abnormal (AB)
Foraging	Eat food or actively searching for food (Ross et al., 2011)	Locomotion/feeding LOC/FE
Vigilance	Visual scanning of the surroundings beyond the immediate vicinity (Treves, 2000)	VIG

Notes. AZA, 2010; Birkett, & Newton-Fisher, 2011, pg. 3; CHCI Archives; Jensvold, Buckner, & Stadtner, 2010; Goodall, 1989; Khan, 2013; Mulcahy, 2001; Parr, Cohen, & de Waal, 2005; Pederson, King, & Landau, 2005; Ross et al., 2011; Treves, 2000; Troisi, 2002

During each 10 minute sample, I continuously recorded the location of the focal chimpanzee indicating whether the focal was indoors or outdoors, and whether they were in view of the visitors regardless of visitor presence. Locations were scored as green house, playroom, front rooms (one through four), and Young's Hill. Two of the three recorded locations (green house and Young's Hill) were in view of visitors.

During each focal sample, I continuously recorded proximity between the focal chimpanzee and other chimpanzees. Close proximity for this study was identified as time spent in the vicinity of other individuals within arm's reach (Zihlman, et al., 2008) without physical contact.

Reliability

As an intern at CSNW, I am required to pass several exams for both chimpanzee identification and knowledge of chimpanzee behavior. In the winter of 2015 I was considered reliable for chimpanzee identification. Prior to data collection in Spring 2015, I was considered reliable for accurate identification of chimpanzee behavior.

CHAPTER IV

ANALYSIS

For each chimpanzee, frequency and durations of behaviors, location duration, and time spent in proximity were summed on tour and non-tour days. I then compared durations for each condition and analyzed them using chi square goodness of fit tests on VassarStats.net in order to test for significant deviation from the expected proportion on tour versus non-tour days.

I also analyzed survey data collected on visitor experience. After each tour was complete, CSNW offered an optional online survey. I reviewed 75 submitted surveys (15 questions), see Appendix A. Three questions were yes/no and one was quantified by summing categorized prices. Information from the surveys was then compared to the statistical results for the chimpanzee behavioral data.

CHAPTER V

RESULTS

I observed seven chimpanzees for 42 days (July 3rd – September 14th). I collected 60 hours of data on tour days (condition one) over the course of 24 days and 45 hours of data on non-tour days (condition two) over the course of 18 days. Because of the unequal amounts of data for each condition, I excluded 12 randomly selected samples from tour days for each chimpanzee to match the total time observed for each chimpanzee in both conditions. For each chimpanzee, I analyzed a total of 720 minutes of observation (360 minutes on tour days, 360 minutes on non-tour days). I ran chi square goodness of fit tests to compare each chimpanzee's behavioral durations on tour and non-tour days in affiliative, abnormal, aggressive, foraging (on Young's Hill), vigilance, time spent in proximity with other individuals, time spent in locations indoor and outdoor, and time spent in locations that are in view of visitors. Each test has one degree of freedom, and p was set at 0.05. Durations, chi square and p values for each chimpanzee are listed in Appendix B.

Reliability

To test intra-observer reliability, I recoded 10% of the total samples on both tour and non-tour days for each chimpanzee; seven samples per chimpanzee with a total of 49 recoded samples. I compared the total number of matches for all occurrence behaviors and time stamps from all seven samples, for each chimpanzee. Ethogram behaviors were 98% reliable and time stamps were 95% reliable.

Tests showed significant differences in the durations of affiliation for three of the seven chimpanzees. Burrrito, Foxie, and Jody spent less time engaging in affiliative

behaviors on tour days. However, Annie, Jamie, Missy, and Negra did not show a significant difference in affiliation on tour and non-tour days.

Tests showed significant differences in the durations of abnormal behaviors for three of the seven chimpanzees. Annie and Foxie spent less time performing self-directed behaviors on tour days. Negra spent more time performing self-directed behaviors on tour days. Burrrito, Jamie, Jody, and Missy did not show a significant difference in the durations of abnormal behaviors on tour and non-tour days.

Due to the low overall durations of aggression observed for the seven chimpanzees, I could not perform statistical analyses for six of the seven chimpanzees. The test results for Burrrito showed a significant difference in duration of aggressive behaviors with more time spent engaging in aggressive behaviors on tour days.

The tests showed no significant differences in foraging duration on Young's Hill for any chimpanzees. Tests showed significant differences in durations of vigilance for four of the seven chimpanzees. Burrrito, Foxie, Missy, and Negra spent more time vigilant on tour days. Annie, Jamie, and Jody did not show a significant difference in durations of vigilance on tour and non-tour days.

Only Foxie showed a significant difference in duration of time spent in proximity to other individuals between tour and non-tour days. She spent more time in proximity to other individuals on tour days. Annie, Burrrito, Jamie, Jody, Missy, and Negra did not show a significant difference in duration of time spent in proximity to other individuals on tour and non-tour days.

Annie and Burrrito showed significant differences in duration of time spent indoors between tour and non-tour days. Annie spent less time indoors on tour days.

Burrito spent more time indoors on tour days. Foxie, Jamie, Jody, Missy, and Negra did not show a significant difference in duration of time spent indoors on tour and non-tour days.

Only Burrito showed a significant difference in duration of time spent outdoors between tour and non-tour days. He spent less time outdoors on tour days. Annie, Foxie, Jamie, Jody, Missy, and Negra did not show a significant difference in duration of time spent outdoors on tour and non-tour days.

Burrito and Missy showed significant differences in duration of time spent in locations in view of visitors between tour and non-tour days. Burrito spent less time in view of visitors on tour days, and Missy spent more time in view of visitors on tour days. Annie, Foxie, Jamie, Jody, and Negra did not show a significant difference in duration of time spent in locations in view of visitors on tour and non-tour days.

A total of 75 guests filled out the optional survey. The majority of guests answered the survey in its entirety with a few guests not answering one or more of the four questions I reviewed for this study. The first question I reviewed asked whether they had learned anything new about CSNW. A total of 69 guests answered this question noting they learned something new about CSNW and or chimpanzee welfare issues (including four guests who had previously attended a tour). The second question I reviewed asked whether they now had a favorite chimpanzee. A total of 65 guests answered this question, 10 of whom said no. The third question I reviewed referred to whether the guests learned something new about chimpanzees in general. A total of 67 guests responded, with only three stating that they did not learn anything new (each of whom noted they were already well-versed in nonhuman primates). The final question

that I reviewed referred to donations, asking what an acceptable tour fee would be (having experienced the tour). A total of 64 guests answered, with 53 guests noting a specific quantity. The majority of suggested fees fell between \$25 and \$50 (30 guests) with a few ranging between \$65 and \$100 (3 guests). More descriptive answers to this question reflected the struggle between the need for funding, education, personal cost to the guests, and their experience.

CHAPTER VI

DISCUSSION

Studies of visitor effects on nonhuman primates have provided evidence for changes in frequencies of nonhuman primate behaviors over time due to exposure to visitors, suggesting a decrease in well-being (Birke, 2002; Blaney & Wells, 2004; Carder & Semple 2008; Chamove et al., 1988; Glaston et al., 1984; Keane & Marples, 2003; Kuhar, 2008; Mallapur et al., 2005; Sherwen et al., 2015; Wells, 2005; Wood, 1998). Limiting environmental stressors can increase captive nonhuman primate well-being. After implementing the summer tour program, CSNW staff are interested in the potential welfare implications of the presence of visitors. I evaluated the frequencies of selected behaviors of the seven chimpanzees that reside at CSNW comparing tour and non-tour days to assess the welfare implications of the summer tours. The behaviors I analyzed have been identified in previous research as sensitive to stress levels. The majority of the behaviors I studied were categorized within three behavioral contexts: aggressive (i.e., display), abnormal (i.e., autogroom), and affiliative (i.e., allogroom). I also evaluated the durations of inter-individual proximity, foraging, and vigilance.

The results indicate that the chimpanzees generally remain unaffected by the presence of visitors. The results did not show consistent changes in durations of behavior among the chimpanzees with values potentially indicating an increase in stress as well as enrichment. Based on the variability among the seven chimpanzees it is difficult to generalize the potential implications of tour visitors.

Where differences existed on tour and non-tour days, most of the chimpanzees only showed one to two significant values. Jamie did not show any significant

differences. Foxie and Burrito showed the most significant differences with four and six significant categories, respectively. The condition (tour or non-tour) in which significantly longer durations were observed and their implications (increase or decrease in welfare), were not consistent for each chimpanzee.

The significant differences I found in the data could indicate an increase in both well-being (i.e., significantly shorter durations of abnormal behaviors on tour days) and stress (i.e., significantly longer durations of aggression on tour days). The variation in the results reflects individual differences among the seven chimpanzees, which may contribute to their behavioral responses on tour and non-tour days. Stoinski et al., (2011) expected variation in their results due to both extrinsic and intrinsic factors that may influence behavioral frequencies among individuals. Individual personality types can “affect the welfare animals experience in captivity” (Watters & Powell, 2011, p. 1). The distinct personalities of the chimpanzees may have influenced the variation in my results, with certain individuals being enriched by the tours while others were mildly stressed by them. Assessing the welfare implications of the tours will require both a consideration of individual personalities (Gosling & John, 1999 as cited in Herrelko, Vick, & Buchanan-Smith, 2012) and their unique life experiences (Huck & Price, 1975 as cited in Carlstead and Shepherdson, 2000) as well as additional data collection over the long term. Consequently, I cannot make a broad conclusion about the welfare implications of the tours.

Affiliation and Inter-Individual Proximity

Affiliation is an important social behavior in chimpanzees (Stumpf, 2011), and both increases and decreases in affiliation have been considered indicative of stress (Hosey, 2005; Cohen et al., 1992). The results from my study indicate that Annie, Jamie, Missy and Negra did not show significant differences in durations of affiliation on tour versus non-tour days. Burrrito, Foxie, and Jody showed a significant difference in affiliation duration with each chimpanzee engaging in significantly less affiliation on tour days. Previous studies on the visitor effect in captive nonhuman primates that analyzed affiliative behaviors have shown similar results (Birke, 2002; Chamove et al., 1988; Glaston et al., 1984; Wood, 1998) with individuals engaging in less affiliation when visitors were present.

In my study, I separated out contact affiliative behaviors from proximity. Inter-individual proximity can be seen as a form of social behavior with affiliative implications (Feldman, 2012; Fraser et al., 2008). To assess the potential impact of the summer tours on the social behavior of the seven chimpanzees, it was important to analyze differences in proximity between the focal individual and other chimpanzees on tour versus non-tour days. Proximity durations for Annie, Burrrito, Jamie, Jody, Missy, and Negra were not significantly different on tour and non-tour days. However, Foxie spent significantly more time in close proximity to other chimpanzees on tour days.

My proximity results show that the benefits of social behavior (contact or not) remain unaffected overall for each chimpanzee. Proximity durations on tour and non-tour days were comparable, suggesting individuals were socializing with and without contact. Although affiliation durations for Burrrito and Jody were low on tour days, proximity

durations were not significantly different on tour versus non-tour days. Affiliation durations for Foxie were significantly lower on tour days and proximity durations were significantly higher on tour days. The two variables were mutually exclusive, suggesting that Foxie's low duration of affiliation was comparable with her high duration of proximity on tour days. Burrito, Foxie, and Jody still maintained social relationships to some degree, whether with physical contact, as seen in grooming, or time spent near one another.

Abnormal

Frequencies of abnormal behaviors at which the physical costs (i.e., physical injury) compromise welfare are no longer considered to be beneficial coping mechanisms (Duncan et al., 2013; Mason, 1991). Elevated rates of abnormal, self directed behaviors have been identified as stress indicators in captive non-human primates (Swaisgood & Shepherdson, 2006). Research on nonhuman primates suggests that abnormal behaviors are part of an adaptive stress response (Troisi, 2002). Previous research has found significant increases in the frequencies of self directed behaviors due to the presence of visitors (Blaney & Wells, 2005; Chamove et al., 1988; Mallapur et al., 2005; Sherwen et al., 2015; Wells, 2005; Wood, 1998).

Burrito, Jamie, Jody, and Missy showed comparable amounts of self directed behaviors on tour and non-tour days. However, Annie, Foxie, and Negra showed significant differences in self directed behaviors. The total duration of self directed behaviors was longer on tour days for Negra but shorter on tour days for Annie and Foxie.

Based on the potentially harmful effects of self directed behaviors and welfare implications of stress (Duncan et al., 2013; Swaisgood & Stepherdson, 2006), potential mitigation measures may be taken to decrease the presence of stress for Negra (i.e., limiting both the size and frequency of the tours throughout the summer months). In contrast to the welfare implications for Negra, the tours may be enriching for Annie and Foxie as reflected in their lower durations of self directed behaviors in the presence of visitors. Environmental enrichment, such as human presence, has been correlated with decreases in abnormal behaviors (Claxton, 2011; Swaisgood & Stepherdson, 2007). Based on the variation in my results in durations of abnormal behaviors, it may be accurate to conclude that for the majority of the chimpanzees, abnormal behaviors did not increase on tour days and generalizations of the welfare implications cannot be made.

Aggression

Observations of aggression were low in my study. Out of 5,040 minutes of observation for all chimpanzees, the aggression duration was only 24 minutes. As a result of the low durations, I could not conduct statistical tests for Annie, Foxie, Jamie, Jody, Missy, and Negra. Aggression on tour and non-tour days could only be analyzed for Burrito. Similar to findings from previous visitor effect research, the results showed that Burrito engaged in significantly more aggression on tour days.

The sampling schedule used for my study (1200-1436) may have had an additional impact on the low frequencies of aggression observed. For example, if my samples had been collected between morning (0900) and evening (1700), the frequencies

of aggression may have fluctuated. Displays and arousal are common in the morning hours.

The scheduled events within the sanctuary that occur on both tour and non-tour days may have been confounding factors in durations of aggressive behaviors (i.e., changes in room availability, guests arriving, forage prepared and laid out, and movement of guests to the viewing deck). Arousal during these events is common. However, because these scheduled events were fixed, any deviation from the expected frequency of aggression on tour days could be attributed to the presence of visitors. Burrrito underwent oral surgery mid-summer, which could be another confounding factor that may have influenced his durations of aggression on both tour and non-tour days.

Based on the behavioral repertoire of a male chimpanzee (Stumpf, 2011), Burrrito's aggressive behaviors may still fall within an expected range. When considering the physical harm that may be associated with aggression, it was important to consider contact versus non-contact aggression for Burrrito. The total sum of Burrrito's aggression on tour and non-tour days was 13 minutes and 33 seconds, with 10 seconds of contact aggression (3 seconds on tour days and 7 seconds on non-tour days). The remaining 13 minutes and 23 seconds was non contact aggression in the form of display. Similar to previous research, this may suggest low impact on physical welfare (Stoinski et al., 2011). Very low durations paired with very little physical contact make it difficult to infer the welfare implications of Burrrito's aggression.

Foraging on Young's Hill

After decades of confinement in biomedical facilities, CSNW provides the chimpanzees with opportunities to engage in species-typical behaviors seen in the wild, such as foraging (Stumpf, 2011). Encouraging foraging behaviors is important for well-being (Pruetz & McGrew, 2001, Carlstead & Shepherdson, 2000; Morgan & Tromborg, 2007; Wemelsfelder & Birke 1997) and is a priority at CSNW. My analysis of foraging durations on Young's Hill was important for welfare assessments. Based on previous research, I predicted durations of foraging would be lower when visitors were present (Birke, 2002; Clark et al., 2011; Hosey, 2000). The results from my study do not show a significant difference in foraging on tour days versus non-tour days for any of the seven chimpanzees. This was an important finding based on welfare implications and inferences about the potential visitor effect and maintaining foraging behaviors (Morgan & Tromborg, 2007; Pruetz & McGrew, 2001; Wemelsfelder & Birke, 1997).

Vigilance

Treves (2000) defines vigilance as the visual scanning of the surroundings beyond the immediate vicinity. Previous research on vigilance in wild populations of chimpanzees suggests that the potential function of vigilance is related to protection and warning of danger (Treves, 2000; Kutsukake, 2005) and it is a potential fear response (Claxton, 2011). An increase in vigilance may suggest an increase in stress (Treves, 2000; Kutsukake, 2005). However, welfare implications are difficult to assess (Davey, 2007). Inferring physical cost associated with long durations of vigilance is not straight forward, unless the individual is vigilant rather than foraging (Claxton, 2011). Vigilance

could indicate that a stimulation within the environment is a form of interest or stress (Sherwen, Magrath, Butler, & Hemsworth, 2015). Research on captive nonhuman primate welfare has suggested that encouraging species-typical behaviors such as vigilance, through environmental enrichment, can increase welfare (Pruetz & McGrew, 2001). Clark et al. (2011) considered both positive and negative visitor-directed vigilance to assess well-being in the presence of large crowds. Based on these concepts, it may be accurate to infer that vigilance towards the guests on tour days may be enriching and or stressful indicating a potential increase or decrease in well-being.

However, I cannot fully attribute the significant differences in vigilance to the presence of visitors. Vigilance both indoors and outdoors may have been directed at a number of focal points. As stated above, the sanctuary's scheduled events (i.e., changes in room availability, guests arriving, forage prepared and laid out, and movement of guests to the viewing deck) may have influenced vigilance for Burrito, Foxie, Missy, and Negra. However, because these scheduled events were fixed, any deviation from the expected frequency of vigilance on tour days could be attributed to the presence of visitors. It is not clear as to whether the significantly longer durations of vigilance on tour days can be fully attributed to the tours; if so, it is difficult to generalize welfare implications based on the potential for enrichment and or stress.

Location Indoor and Outdoor

CSNW was designed to offer a variety of spaces for the chimpanzees to spend their time. I categorized the four sections of the enclosure as indoor (playroom and front rooms) and outdoor (green house and Young's Hill) to assess whether location differed

on tour and non-tour days. Foxie, Jamie, Jody, Missy, and Negra did not show significant differences in location on tour and non-tour days, but Annie and Burrito showed significant differences in location on tour versus non-tour days. Annie spent significantly less time indoors on tour days. The visitors may have been a form of enrichment encouraging less time indoors when present.

By contrast, Burrito spent significantly more time indoors and less time outdoors on tour days. Burrito may have spent less time in the outdoor locations and more time in the indoor locations on tour days to avoid the visitors. However, results for Burrito's foraging behaviors indicate his potential avoidance of guests did not have an overall impact on his welfare. There was no significant difference in durations of foraging (which occurs in view of the visitors) on tour and non-tour days. It may be accurate to infer his energy budget remains relatively unaffected. It is important to consider other factors in the environment that may have influenced subsets of his location durations. Temperatures during the summer months varied greatly from high heat (above 90° F) to rain. A subset of Burrito's time spent indoors may have been in avoidance of the weather, rather than visitors alone. The day following his oral surgery was a tour day and he remained indoors during his recovery. Due to these elemental factors and results for Burrito's foraging, generalizations about the influence of tours on his location use are difficult to make.

In View of Visitors

After decades of confinement and exploitation by humans, it is important for captive nonhuman primates to exercise their free will for privacy (Carlstead &

Stepherdson, 2000; Sherwen et al., 2015). The blueprints for CSNW allow for the chimpanzees to remain out of view of caregivers, visitors, and other chimpanzees. During my observations I noted whether the chimpanzees were in locations that would be in view of the visitors (regardless of the presence or absence of visitors) to test for a significant difference in their use of these spaces on tour versus non-tour days. In the indoor locations, chimpanzees were out of view of the visitors when they were in the parking lot and at the viewing deck. In the outdoor locations, multiple spaces allowed the chimpanzees to be in view or out of view of visitors. Depending on their location, chimpanzees could choose to be outdoors and remain out of view of the visitors.

Annie, Foxie, Jamie, Jody, and Negra did not show significant differences in durations of time spent in locations in view of the visitors, but Burrito and Missy showed a significant difference. Burrito spent significantly less time in locations that would be visible to visitors on tour days. These results are consistent with Burrito's low outdoor durations on tour days. He may have been avoiding locations visible to visitors on tour days due to potential stress induced by the visitors. However, his durations of foraging remained unaffected by the tours, and his ability to remain out of view of visitors when he chose to be outdoors may indicate his well-being may be unaffected. Missy spent significantly more time in locations that were visible to visitors on tour days, suggesting that Missy was not negatively affected by the tours and was possibly enriched by the visitors' presence. For the majority of the individuals in my study, location preference in or out of view of visitors did not differ on tour or non-tour days.

Tour Survey

The tour survey provided evidence that the summer tour program is effective. First, in educating the public about CSNW, the seven chimpanzees that reside there, and chimpanzee welfare in general. Answers to question #8 showed that 100% of visitors, including four guests who were repeat visitors, learned something new about CSNW. Answers to question #10 also showed that the tours were very informative, with only three guests stating that they did not learn anything new about chimpanzees and welfare issues in general. Each of these three individuals noted that they were well-versed in nonhuman primates.

Secondly, the tour survey provided evidence that the summer tour program is effective at encouraging empathy. Well over half of the 65 guests who responded to question #9 stated that they had a favorite chimpanzee or that they could not choose, caring for them all equally. The nine guests who responded no, does not necessarily indicate that they do not care for the chimpanzees, rather, it means they had no favorite.

Finally, the survey provided evidence that the summer tour program is effective at maintaining financial support. Half of the guests who responded to question #14 recommended donation fees of moderate value. Those who did not suggest a fee described their hesitation, noting a common conundrum: the need for funding and support for CSNW and the need to maintain such funding, but not deterring guests by asking for fees that may be unaffordable to the general public. Visitors' answers suggested that a high fee might deter individuals who may be great resources for CSNW in the future, while at the same time noted the need for a strong source of funding. Nevertheless, tour

donations are a source of financial support, facilitating a valuable experience that does not seem to be affecting the chimpanzees' welfare.

Responses to the survey show that the strongest benefits of the tours are education and empathy. The financial gain from the tours may be indirect as seen in an increase in donorship throughout the year, rather than a particular price at the time of the tour. The behavioral data from my study did not show consistent changes in durations of behavior suggestive of stressful states. Paired with an increase in education and empathy for chimpanzee welfare and CSNW, it is reasonable to suggest that the summer tours contribute benefits that outweigh potential costs of the tours.

CHAPTER VII

CONCLUSION

Significant differences in behavioral durations and the welfare based inferences (i.e., increases or decrease on tour or non-tour days) were not consistent across all seven chimpanzees. Because some durations indicated stress while others indicated enrichment, future decisions regarding the summer tours can consider individual differences.

“Identifying the sensory stimuli that mediate the visitor effects on primates may be critical in developing interventions that optimize animal welfare” (Sherwen et al. 2015, p. 66). The results from my study will provide CSNW staff with necessary information unique to each chimpanzee to mitigate any potential stress induced by the visitors, while still encouraging stimulation for those chimpanzees who may have been enriched by the tours. This may allow for simple mitigation measures to be taken (i.e., tour size and frequency) if CSNW finds necessary, rather than eradication of the tour program.

For the scope of my study, behavioral durations were not analyzed in accordance with the varying tour sizes. Tour size varied throughout the summer between 2 and 20 guests. Further research on the visitor effect at CSNW can consider tour size to determine whether number of guests impacts chimpanzee behavior. Future studies can also analyze a broader repertoire of the chimpanzee behaviors across a longer timespan. After a few tour seasons, behavioral data can be aggregated for each chimpanzee individually, providing a more comprehensive dataset. Having a set schedule of tour days may allow for equal amounts of data per condition with more accurate time matched samples.

Future research can consider more detailed observations. In order to assess more accurate measures of welfare it would be informative to have details as to where

aggressive behaviors were directed (i.e., within group or towards guests) and whether the aggression was contact or non contact. Proximity can be analyzed in regards to room availability in order to assess potential causes. Methods from this study can be applied to other sanctuary environments in order to contribute to a large body of data on in the presence and absence of visitors.

Due to the recent developments at CSNW and the expansion of the facility to accommodate a new group of chimpanzees, the structure and frequency of tours may change. This new development may increase visitation to the sanctuary, and further research on visitor effects may aid in maintaining the welfare of all chimpanzees that will reside at CSNW.

REFERENCES

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behavior*, *49*, 227-267.
- AZA Ape Taxon Advisory Group., & AZA Animal Welfare Committee. (2010). In: Ross, S., & McNary, J. (Eds.), *Chimpanzee (Pan troglodytes) Care Manual*. Silver Spring: Association of Zoos and Aquariums.
- Baker, K. C. (2004). Benefits of positive human interaction for socially-housed chimpanzees. *Animal Welfare*, *13*(2), 239-245.
- Barnard, C. J., & Hurst, J. L. (1996). Welfare by design: The natural selection of welfare criteria. *Animal Welfare*, *5*, 405-433.
- Beck, B. B. (2010). Chimpanzee orphans: Sanctuaries, reintroduction, and cognition. In Lonsdorf, E., Ross, S., Matsuzawa, T. (Eds.), *The mind of the chimpanzee: Ecological and experimental perspectives* (332-346). Chicago: University of Chicago Press.
- Beck, B., Walkup, K., Rodrigues, M., Unwin, S., & Stoinski, D. (2007). Best practice guidelines for re-introduction of great apes. Gland, Switzerland: SSC Primate Specialist Group of the World Conservation Union.
- Bernstein, I. S., & Gordon, T. P. (1974). The function of aggression in primate societies. *American Scientist*, *62*(3), 304-311.
- Berridge, C. W., Mitton, E., Clark, W., & Roth, R. H. (1999). Engagement in a non-escape (displacement) behavior elicits a selective and lateralized suppression of frontal cortical dopaminergic utilization in stress. *Synapse*, *32*, 187-197.
- Birke, L. (2002). Effects of browse, human visitors and noise on the behaviour of captive orangutans. *Animal Welfare*, *11*, 189-202.
- Birkett L. P., & Newton-Fisher N. E. (2011) How abnormal is the behaviour of captive, zoo-living chimpanzees? *PLoS ONE*, *6*(6), e20101.
doi:10.1371/journal.pone.0020101
- Blaney, E. C., & Wells, D. L. (2004). The influences of a camouflage net barrier on the behaviour, welfare, and public perceptions of zoo-housed gorillas. *Animal Welfare*, *13*, 111-118.
- Bloomsmith, M. A., Alford, P. L., & Maple, T. L. (1988). Successful feeding enrichment for captive chimpanzees. *American Journal of Primatology*, *16*, 155-164.

- Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L.J.,...Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology and Behavior*, *92*, 375-397.
- Broom, D. M. (1983). Stereotypies as animal welfare indicators. *Indicators Relevant to Farm Animal Welfare*, 81-87.
- Broom, D. M. (1986). Indicators of poor welfare. *British veterinary journal*, *142*(6), 524-526.
- Brune, M., Brune-Cohrs, U., McGrew, W. C., & Preuschoft, S. (2006). Psychopathology in great apes: Concepts, treatment options and possible homologies to human psychiatric disorders. *Neuroscience and Behavioral Reviews*, *30*, 1246-1259.
- Carder, G., & Semple, S. (2008). Visitor effects on anxiety in two captive groups of western lowland gorillas. *Applied Animal Behaviour Science*, *115*, 211-220.
- Carlstead, K., & Shepherdson, D. (2000). Alleviating stress in zoo animals with environmental enrichment. *The biology of animal stress: Basic principles and implications for animal welfare*. In G. P. Moberg & J. A. Mench (Eds.) (pp.337-354). New York, NY: CABI Publishing.
- Chamove, A., Hosey, G., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo Biology*, *7*, 359-369.
- Chelluri, G. I., Ross, S. R., & Wagner, K. E. (2013). Behavioral correlates and welfare implications of informal interactions between caregivers and zoo-housed chimpanzees and gorillas. *Applied Animal Behaviour Science*, *147*, 306-315.
- Chimpanzee and Human Communication Institute Records. MS009-01-01. Central Washington University Archives and Special Collection. Central Washington University.
- Chimpcare. (2016). Where are our amazing chimpanzees in the United States. Retrieved from <http://www.chimpcare.org/map>
- Clark, F. E., Fitzpatrick, M., Hartley, A., King, A., Lee, T., Routh, A.,...George, K. (2011). Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology*, *30*, 1-16.
- Clark, F. E. (2011). Great ape cognition and captive care: can cognitive challenges enhance well-being?. *Applied Animal Behaviour Science*, *135*, 1-12.

- Clarke, A. S., Juno, C. J., & Maple, T. L. (1982). Behavioral effects of a change in the physical environment: A pilot study of captive chimpanzees. *Zoo Biology, 1*, 371-380.
- Claxton, A. M. (2011). The potential of the human-animal relationship as an environmental enrichment for the welfare of zoo-housed animals. *Applied Animal Behaviour Science, 133*, 1-10.
- Clubb, R., & Mason, G. J. (2007). Natural behavioural biology as a risk factor in carnivore welfare: how analyzing species differences could help zoos improve enclosures. *Applied Animal Behaviour Science, 102*, 303-328.
- Coe, J. C., Scott, D., & Lukas, K. E. (2009). Facility design for bachelor gorilla groups. *Zoo Biology, 28*, 144-162.
- Cohen, S., Kaplan, J. R., Cunnick, J. E., Manuck, S. B., & Rabin, B. S. (1992). Chronic social stress, affiliation, and cellular immune response in nonhuman primates. *Psychological Science, 3*(5), 301-304.
- Cook, S., & Hosey, G. R. (1995). Interaction sequences between chimpanzees and human visitors. *Zoo Biology, 14*, 431-440.
- Crofoot, M.C., Lambert, T.D., Kays, R., & Wikelski, M.C. (2010). Does watching a monkey change its behaviour? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Animal Behaviour, 80*, 475-480.
- Darken-Schultz, N. J., Pape, R. M., Tannenbaum, P. L., Saltzman, W., & Abbott, D. H. (2004). Novel restraint system for neuroendocrine studies of socially living common marmoset monkeys. *Laboratory Animals, 38*, 393-405.
- Davey, G. (2005). The “visitor effect”. *Zoos' Print Journal, 20*(6), 1900-1903.
- Davey, G. (2006). Visitor behavior in zoos: A review. *Anthrozoos, 19*(2), 143-157.
- Davey, G. (2007). Visitors' effects on the welfare of animals in the zoo: A review. *Journal of Applied Animal Welfare Science, 10*(2), 69-183.
- Davis, N., Schaffner, C. M., & Smith, T. E. (2005). Evidence that zoo visitors influence HPA activity in spider monkeys (*Ateles geoffroyii rufiventris*). *Applied Animal Behaviour Science, 90*, 131-141.
- Dawkins, M. S. (2004). Using behaviour to assess animal welfare. *Animal Welfare, 13*, 3-7.

- de Almeida, R. M. M., Ferrari, P. F., Parmigiani, S., & Miczek, K. A. (2005). Escalated aggressive behavior: Dopamine, serotonin and GABA. *European Journal of Primatology*, *526*, 51-64.
- Duboscq, J., Agil, M., Engelhardt, A., & Thierry, B. (2014). The function of postconflict interactions: New prospects from the study of a tolerant species of primate. *Animal Behaviour*, *87*, 107-120.
- Duncan, L. M., Jones, M. A. von Lierop, M., & Pillay, N. (2013). Chimpanzees use multiple strategies to limit aggression and stress during spatial density changes. *Applied Animal Behaviour Science*, *147*, 159-171.
- Etim, N. N., Offiong, E. A., Eyoh, G. D., & Udo, M. D. (2013). Stress and animal welfare: An uneasy relationship. *European Journal of Advanced Research in Biological and Life Sciences*, *1*(1), 9-16.
- Feldman, R. (2012). Oxytocin and social affiliation in humans. *Hormones and behavior*, *61*(3), 380-391.
- Fernandez, E. J., Tamborski, M. A., Pickens, S. R., & Timberlake, W. (2009). Animal-visitor interactions in the modern zoo: Conflicts and interventions. *Applied Animal Behaviour Science*, *120*, 1-8.
- Fouts, R. S., Fouts, D. H. & Waters, G. (2002). The ethics and efficacy of biomedical research in chimpanzees with special regard to HIV research. In: Fuentes, A., & Wolfe, L.D. (Eds.) *Primates Face to face: the conservation implications of human-nonhuman primate interconnections*, 45-60. New York: Cambridge University Press
- Frankham, R., Hemmer, H., Ryder, O. A., Cothran, E. G., Soule, M. E., Murray, N. D., Snyder, M. (1986). Selection in captive populations. *Zoo Biology*, *5*, 127-138.
- Fraser, O. N., Schino, G., & Aureli, F. (2008). Components of relationship quality in chimpanzees. *Ethology*, *114*(9), 834-843.
- Glaston, A. R., Geilvoet-Soeteman, E., Hora-Pecek, E., & van Hooff, J. A. R. A. M. (1984). The influence of the zoo environment on social behavior of groups of cotton-top tamarins, *Saguinus oedipus oedipus*. *Zoo Biology*, *3*, 241-253.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, Massachusetts, & London, England: Belknap Press of Harvard University Press.
- Ha, J.C., Robinette, R. L., & Davis, A. (2000). Survival and reproduction in the first two years following a large-scale primate colony move and social reorganization. *American Journal of Primatology*, *50*, 131-138.

- Herbinger, I., Boesch, C., & Rothe, H. (2001) Territory characteristics among three neighboring chimpanzee communities in the Tai National Park, Ivory Coast. *International Journal of Primatology*, 22, 143-167.
- Herrelko, E. S., Vick, S. J. Buchanan-Smith, H. (2012). Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare. *American journal of primatology*, 74(9), 828-840.
- Honess, P. E., & Marin, C. M. (2006). Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience and Biobehavioral Reviews*, 30, 390–412.
- Honess, P. E., & Marin, C. M. (2006). Enrichment and aggression in primates. *Neuroscience and Biobehavioral Reviews*, 30, 413-436.
- Hosey, G. R. & Druck, P. L. 1987. The influence of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science*, 18, 19-29.
- Hosey, G. R. (2000). Zoo animals and their human audiences: What is the visitor effect?. *Animal Welfare*, 9, 343-357.
- Hosey, G. R. (2005). How does the zoo environment affect the behaviour of captive primates?. *Applied Animal Behaviour Science*, 90, 107–129.
- Hosey, G. (2008). A preliminary model of human-animal relationships in the zoo. *Applied Animal Behavior Science*, 109, 105-127.
- The Humane Society of the United States. (2016). Questions and answers about monkeys used in research. Retrieved from http://www.humanesociety.org/animals/monkeys/qa/questions_answers.html
- Jensvold, M. L. A. (2008). Chimpanzee (*Pan troglodytes*) responses to caregiver use of chimpanzee behaviors. *Zoo Biology*, 27, 345-359.
- Jensvold, M. L. A., Buckner, J.C., & Stadtner, G.B. (2010). Caregiver-chimpanzee interactions with species-typical behaviors. *Interaction Studies*, 11(3), 396-409.
- Keane, C., Marples, N. (2003). The effects of zoo visitors on gorilla behaviour. In: Gilbert, T.C. (Eds.), *Proceedings from 2003: The 5th Annual Symposium on Zoo Research*, (144-154). Winchester, UK: Marwell Zoological Park.
- Khan, B. N. (2013). Impact of captivity on social behavior of chimpanzee (*Pan troglodytes*). *The Journal of Animal & Plant Sciences*, 23(3), 779-785.

- Klailova, M., Hodgkinson, C., & Lee, P. C. (2010). Behavioral responses of one western lowland gorilla (*Gorilla gorilla, gorilla*) group at Bai Hokou, Central African Republic, to tourists, researchers and trackers. *American Journal of Primatology*, 72, 897-906.
- Knight, J. (2009). Making wildlife viewable: habituation and attraction. *Society and Animals*, 17, 167-184.
- Kranendonk, G., & Schippers, E. P. (2014). A pilot study on the effects of a change in behavioural management on the behaviour of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, 160, 127-137.
- Kuhar, C. W. (2008). Group differences in captive gorillas' reaction to large crowds. *Applied Animal Behaviour Science*, 110, 377-385.
- Lahm, S. A. (1981). The effects of public density and harassment on primate behavior at the San Diego Zoo. (unpublished manuscript cited in Chamove et al., 1988).
- Lambeth, S. P., Bloomsmith, M. A., & Alford, P. L. (1997). Effects of human activity on chimpanzee wounding. *Zoo Biology*, 16, 327-333.
- Lilienfeld, S. O., Gershon, J., Duke, M., Marino, L., & de Waal, F. (1999). A preliminary investigation of the construct of psychopathic personality (psychopathy) in chimpanzees (*Pan troglodytes*). *Journal of comparative psychology*, 113(4), 365.
- Logan, C. J., Emery, N. J., & Clayton, N. S. (2012). Alternative behavioral measures of postconflict affiliation. *Behavioral Ecology*, 1-15.
- Lopresti-Goodman, S. M., Kameka, M., & Dube, A. (2013). Stereotypical behaviors in chimpanzees rescued from the African bushmeat and pet trade. *Behavioral Science*, 3, 1-20.
- Maestriperi, D. (2010). Neurobiology of social behavior. *Primate Neuroethology*. Oxford University Press, New York, 359-384.
- Mallapur, A., Anindya, S., & Waran, N. (2005). Influence of visitor presence on the behaviour of captive lion-tailed macaques (*Macaca silenus*) housed in Indian zoos. *Applied Animal Behaviour Science*, 94, 341-352.
- Mason, G. J. (1991). Stereotypies: a critical review. *Animal Behaviour*, 41, 1015-1037.
- Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behavior. *Applied Animal Behaviour Science*, 102, 163-188.

- Mason, G., Burn, C. C., Dallaire, J. A., Kroshko, J., Kinkaid, H. M., & Jeschke, J. M. (2013). Plastic animals in cages: behavioural flexibility and responses to captivity. *Animal Behaviour*, 85, 1113-1126.
- Mason, P. (2000). Zoo Tourism: The need for more research. *Journal of Sustainable Tourism*, 8(4), 333-339.
- McDougall, P. (2012). Is passive observation of habituated animals truly passive?. *Journal of Ethology*, 30, 219-223.
- McGrew, W. C. (1981). Social and cognitive capabilities of nonhuman primates: lessons from the wild to captivity. *International Journal for the Study of Animal Problems*, 2, 138-149.
- McPhee, M. E., & Carlstead, K. (2010). The importance of maintaining natural behaviors in captive mammals. *Wild Mammals In Captivity: Principles and Techniques For Zoo Management*, 303-313.
- Messenger, G. (2015). *A disgraceful era in our treatment of chimps ended today*. Retrieved from <https://www.thedodo.com/hope-arrives-for-chimpanzees-1348050214.html>
- Mitchell, G., Herring, F., Stephanie, O., Tromborg, C., Dowd B., Neville, L. E., & Field, L. (1991). Effects of visitors and cages on changes in the behaviors of mangabeys. *Zoo Biology*, 10, 417-423.
- Mitchell, G., Tromborg, C. T., Kaufman, J., Bargabus, R., Rosileen, S., & Geissler, V. (1992). More on the 'influence' of zoo visitors on the behavior of captive primates. *Applied Animal Behaviour Science*, 2, 189-198.
- Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, 102, 262-302.
- Morris, D. (1964). The response of animals to a restricted environment. *Symposia of the Zoological Society of London*, 13, 99-118.
- Mulcahy, J. B. (2001). *Preconflict behavior in a small group of chimpanzees* (Master's thesis). Central Washington University, Ellensburg, WA.
- Newton-Fisher, N., & Lee, P. (2011). Grooming reciprocity in wild male chimpanzees. *Animal Behaviour*, 81, 439-446.
- NCCR, (2009). *NCCR Fact Sheet*. Retrieved from http://dpcpsi.nih.gov/sites/default/files/NPRR_Fact_Sheet_508.pdf

- Odberg, F. O. (1989). Behavioural coping in chronic stress conditions. In: Blanchard, R.J., Brain, P., Blanchard, D.C., Parmigiani, S. (Eds.), *Ethoexperimental approaches to the study of behavior* (229-238). Dordrecht, Boston, & London: Kluwer Academic Publishers.
- Olson, M. V., & Varki, A. (2002). Sequencing the chimpanzee genome: insights into human evolution and disease. *Nature Reviews Genetics*, 4, 20-28.
- Parr, L. A., Cohen, M., & de Waal, F. (2005). Influence of social context on the use of blended and graded facial displays in chimpanzees. *International Journal of Primatology*, 26(1), 73-103.
- Pederson, A. K, King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality*, 39, 534-549.
- Pruetz, J. D., & McGrew, W. C. (2001). What does a chimpanzee need? Using natural behavior to guide the care and management of captive populations. *Care and management of captive chimpanzees*, 17-37.
- Quadros, S., Goulart, V. D. L., Passos, L., Vecci, M. A. M., & Young, R. J. (2014). Zoo visitor effect on mammal behaviour: Does noise matter?. *Applied Animal Behaviour Science*, 156, 78-84.
- Quigley, M. (2007). Non-human primates: The appropriate subjects of biomedical research?. *Journal of Medical Ethics*, 33(11), 655-658.
- Reade, R. S., & Waran, N. K. (1996). The modern zoo: How do people perceive zoo animals? *Animal Welfare*, 47, 109–118.
- Reimers, M., Schwarzenberger, F., Preuschoft, S. (2007). Rehabilitation of research chimpanzees: Stress and coping after long-term isolation. *Hormones and Behavior*, 51, 428-435.
- Rogers, J., Garcia, R., Shelledy, W., Kaplan, J., Arya, A., Johnson, Z.,...Cameron, J. (2006). An initial genetic lineage map of the rhesus macaque (*Macca mulatta*) genome using human microsatellite loci. *Genomics*, 87, 30-38.
- Ross, S. R., Wagner, K. E., Schapiro, S. J., Hau, J., & Lukas, K. E. (2011). 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.
- Rumbaugh, D. M. (1972). Zoos: Valuable adjuncts for instruction and research in primate behavior. *Bioscience*, 22(1), 26-29.

- Sajjad, S., Farooq, U., Anwar, M., Khurshid, A., & Bukhari, S. A. (2011). Effect of captive environment on plasma cortisol level and behavioral pattern of Bengal Tigers (*Panthera tigris tigris*). *Pakistan Veterinary Journal*, 31(3), 195-198.
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, 308, 648-652.
- Sherwen, S. L., Harvey, T. J., Magrath, M. J., Butler, K. L., Fanson, K. V., & Hemsworth, P. H. (2015). Effects of visual contact with zoo visitors on black-capped capuchin welfare. *Applied Animal Behaviour Science*, 167, 65-73.
- Sherwen, S. L., Magrath, M. J., Butler, K. L., & Hemsworth, P. H. (2015). Little penguins, *Eudyptula minor*, show increased avoidance, aggression and vigilance in response to zoo visitors. *Applied Animal Behaviour Science*, 168, 71-76.
- Snyder, R. L. (1975). Behavioral stress in captive animals. *Research in zoos and aquariums*, 41-76.
- Stoinski, T. S., Jaicks, H. F., & Drayton, L. A. (2011). Visitor effects on the behavior of captive western lowland gorillas: the importance of individual differences in examining welfare. *Zoo Biology*, 30, 1-14.
- Stumpf, R. M. (2011). Chimpanzees and bonobos: Inter- and intra- species diversity. In: Campbell, C. J., Fuentes, A., MacKinnon, K. C., Bearder, S. K., & Stumpf, R. M. (Eds.), *Primates in Perspective, 2nd Edition* (340-356). Oxford: Oxford University Press.
- Swaigood, R., & Shepherdson, D. (2006). Environmental enrichment as a strategy for mitigating stereotypes in zoo animals: a literature review and meta-analysis. *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*, 256-285.
- Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, 60(6), 711-722.
- Treves, A., & Pizzagalli, D. (2002). Vigilance and perception of social stimuli: Views from ethology and social neuroscience. *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition*, 463-469.
- Trofimuik, E., & Braszko, J. J. (2015). Ciproxifan differentially modified cognitive impairment evoked by chronic stress and chronic corticosterone administration in rats. *Behavioural Brain Research*, 283, 145-153.
- Troisi, A. (2002). Displacement activities as a behavioral measure of stress in nonhuman primates and human subjects. *Stress*, 5(1), 47-54.

- Watters, J. V., & Powell, D. M. (2012). Measuring animal personality for use in population management in zoos: suggested methods and rationale. *Zoo Biology*, 31(1), 1-12.
- Wells, D. (2005). A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, 93, 13-17.
- Wemelsfelder, F., & Birke, L. I. A. (1997). Environmental challenge. In: Appleby, M.C., & Hughes, B.O. (Eds.), *Animal Welfare* (35-47). Wallingford: CAB International.
- Wobber V., & Hare, B. (2011) Psychological Health of Orphan Bonobos and Chimpanzees in African Sanctuaries. *PLoS ONE* 6(6): e17147. doi:10.1371/journal.pone.0017147.
- Wood, W. (1998). Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes*). *Zoo Biology*, 17, 211-230.
- Yamanashi, Y. & Hayashi, M. (2011). Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of activity budget between wild and captive chimpanzees. *American Journal of Primatology*, 73, 1231-1238.
- Zihlman, A. L., Stahl, D., & Boesch, C. (2008). Morphological variation in adult chimpanzees (*Pan troglodytes verus*) of the Tai National Park, Cote D'Ivoire. *American Journal of Physical Anthropology*, 135, 43-41.

APPENDIX A

Chimpanzee Sanctuary Northwest Visitor Survey

1. Name (optional)
2. Email Address (optional)
3. How did you first learn about Chimpanzee Sanctuary Northwest (CSNW)?
4. How long have you known about CSNW?
5. Are you currently signed up for CSNW's electronic newsletter?
6. Do you follow CSNW's blog?
7. Which staff member led your visit?
- 8. Did you learn new information about CSNW during your visit? (Feel free to share specifics)**
- 9. Do you have a favorite chimp now? If so, and why?**
- 10. Did you learn new information about chimpanzees in general during your visit? (Feel free to share specifics)**
11. What do you think CSNW's greatest need is right now?
12. What was the best part of your visit?
13. What aspects of the visit could be improved?
- 14. Now that you've had the opportunity to visit, what do you think is a reasonable fee or suggested donation per person?**
15. Is there anything else you'd like to share about your experience visiting CSNW or about the sanctuary?

Note: I analyzed the questions in bold.

APPENDIX B

Behavioral Durations, Chi Square, P-Value For Each Chimpanzee

Values	Affiliation	Abnormal	Behavior						
			Aggression	Proximity	Indoor	Outdoor	Forage	Vigilant	In View
<u>Annie</u>									
Duration T	38.40	43.00	0	131	143.05	217.28	52.38	14.00	195.10
Duration NT	50.88	71.76	0	154	181.10	178.90	43.08	12.75	174.38
χ^2	1.48	6.72	—*	1.70	4.24	3.52	0.72	0	1.06
P value	0.22	0.01	—*	0.19	0.04	0.06	0.40	1	0.30
<u>Burrito</u>									
Duration T	16.60	46.66	11.12	127	212.88	146.88	48.96	34.71	135.03
Duration NT	50.63	57.40	0.95	110	131.18	227.66	33.18	7.00	183.61
χ^2	16.98	0.92	6.96	1.08	18.92	17.00	2.66	17.10	7.1
P value	<0.001	0.34	0.01	0.30	<0.001	<0.001	0.10	<0.001	0.01
<u>Foxie</u>									
Duration T	6.25	36.38	5.15	135	168.71	190.35	38.15	27.68	174.86
Duration NT	28.33	59.56	1.26	92	141.28	214.32	39.53	7.60	193.61
χ^2	12.86	5.12	—*	7.78	2.16	0.36	0	10.32	0.86
P value	0.00	0.02	—*	0.01	0.14	0.55	1	0.00	0.35
<u>Jamie</u>									
Duration T	17.26	28.45	2.38	55.00	201.50	156.45	47.51	36.1	138.95
Duration NT	21.83	24.25	0	51.00	219.76	140.23	49.48	23.18	122.98
χ^2	0.32	0.20	—*	0.08	0.70	0.78	0	2.40	0.86
P value	0.57	0.65	—*	0.78	0.40	0.38	1	0.12	0.35
<u>Jody</u>									
Duration T	36.63	62.81	0.48	103.00	201.28	156.71	14.43	11.05	147.76
Duration NT	71.72	53.98	0.20	111.00	181.36	177.73	9.20	6.92	173.26
χ^2	10.72	0.52	—*	0.22	0.94	1.20	0.76	0.54	1.86
P value	0.00	0.47	—*	0.64	0.33	0.27	0.38	0.46	0.17
<u>Missy</u>									
Duration T	73.10	60.31	1.43	87.00	222.02	135.00	22.73	16.16	128.98
Duration NT	51.33	75.30	0	104.00	238.66	111.33	13.78	5.16	94.98
χ^2	3.56	1.46	—*	1.34	0.54	2.08	1.74	4.70	4.86
P value	0.06	0.23	—*	0.25	0.46	0.14	0.19	0.03	0.03
<u>Negra</u>									
Duration T	8.12	53.30	0.18	114.00	267.75	92.25	9.43	22.90	86.33
Duration NT	6.86	29.52	0	98.00	257.05	102.43	11.53	9.51	92.38
χ^2	0	6.26	—*	1.06	0.18	0.44	0.06	4.74	0.14
P value	1	0.01	—*	0.30	0.67	0.51	0.81	0.03	0.71

Notes. *Low durations could not be analyzed statistically.

T = Tour

NT = Non Tour

APPENDIX C

Graphs of Individual Chimpanzee's Observed Durations

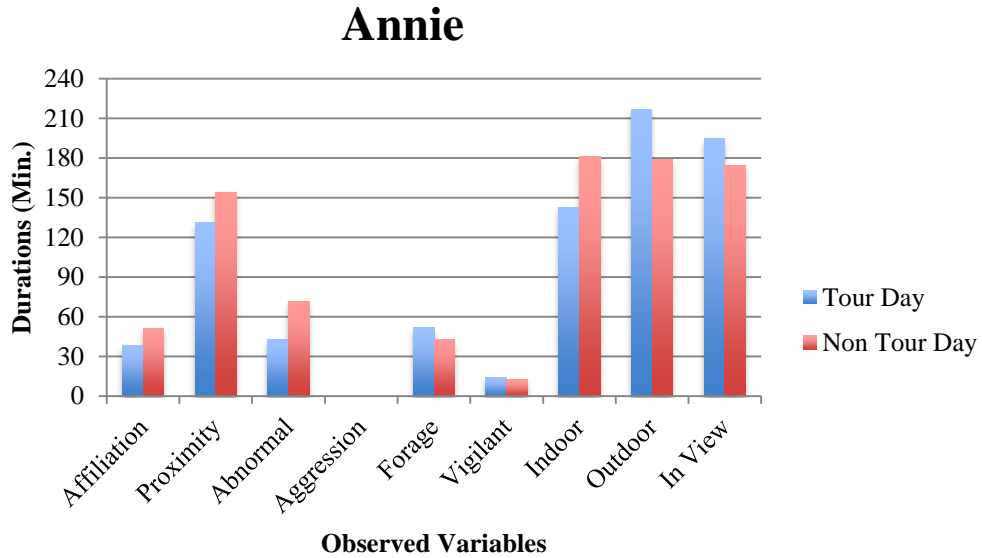


Figure C1. Annie's observed durations

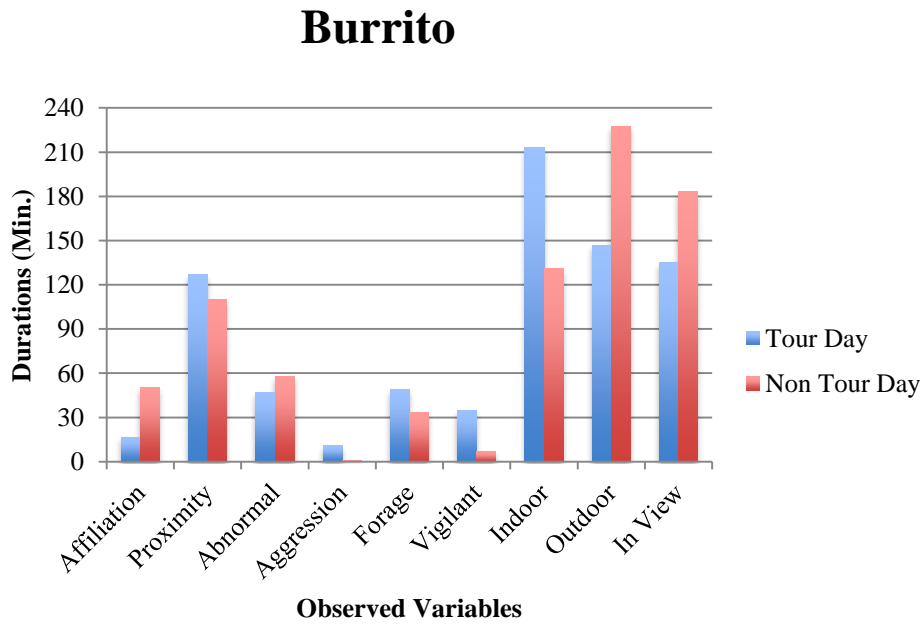


Figure C2. Burrito's observed durations

Foxie

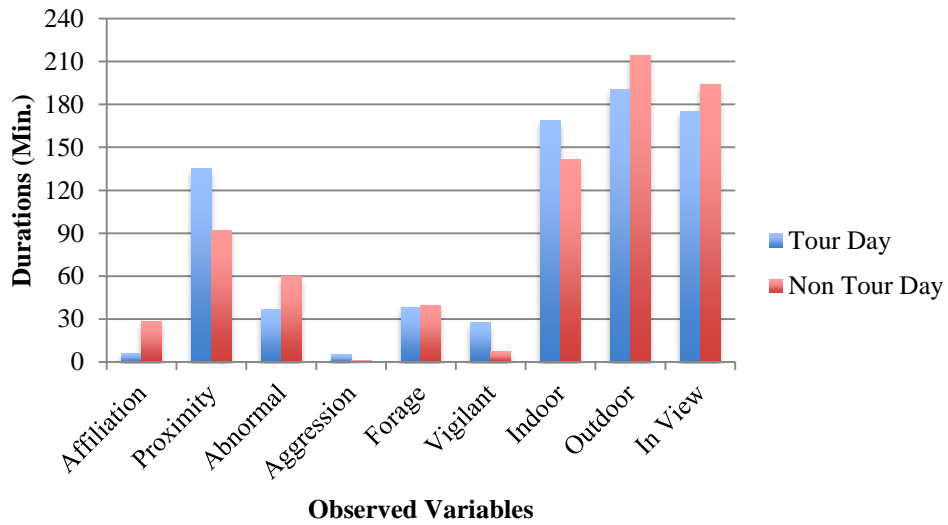


Figure C3. Foxie's observed durations

Jamie

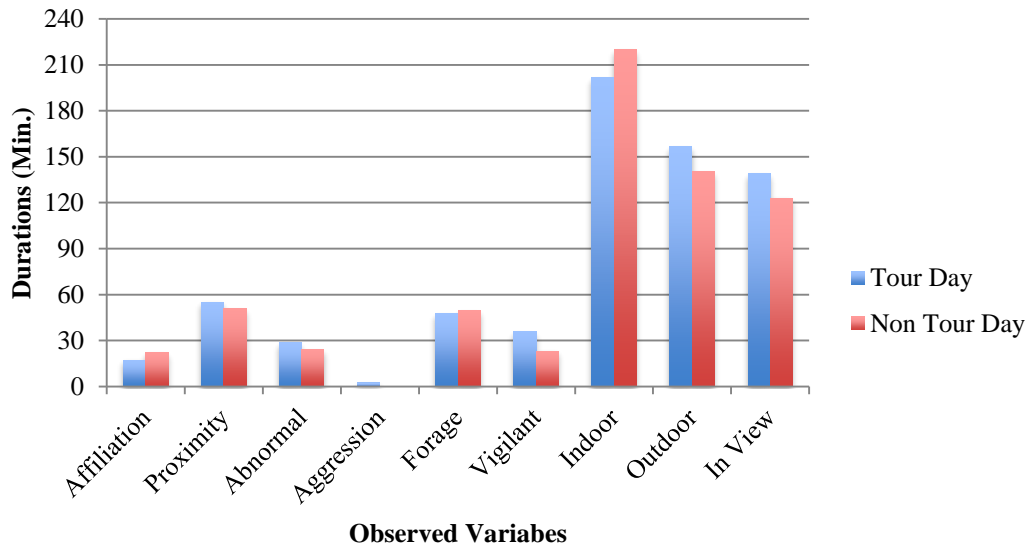


Figure C4. Jamie's observed durations

Jody

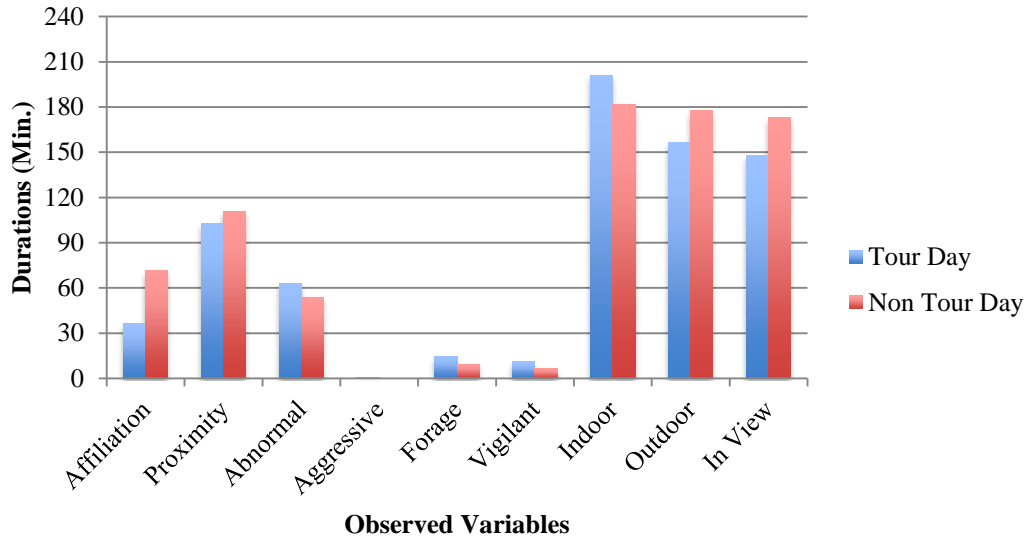


Figure C5. Jody's observed durations

Missy

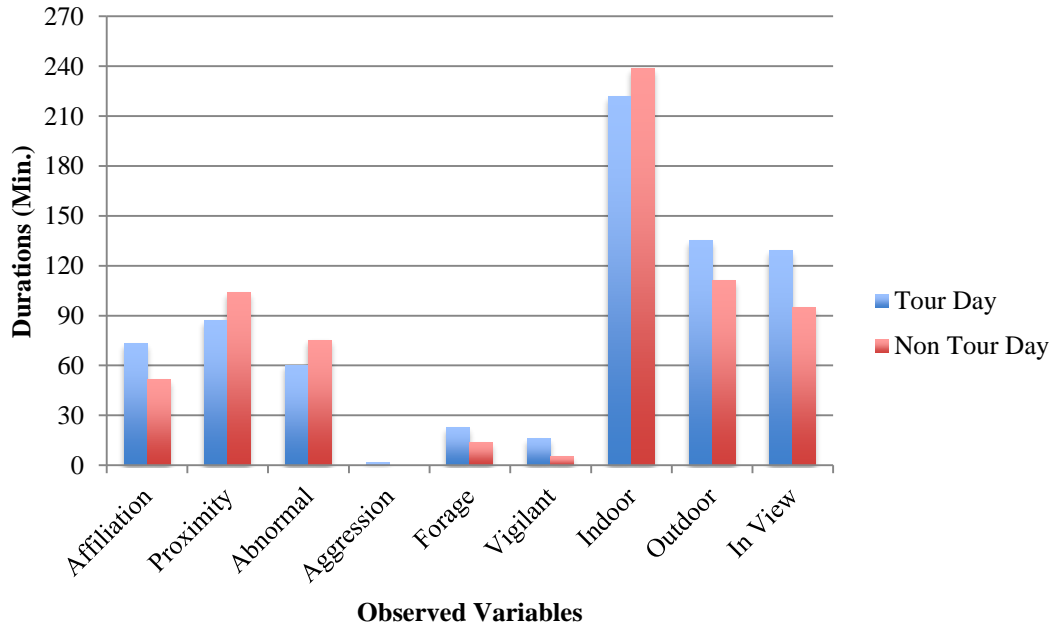


Figure C6. Missy's observed durations

Negra

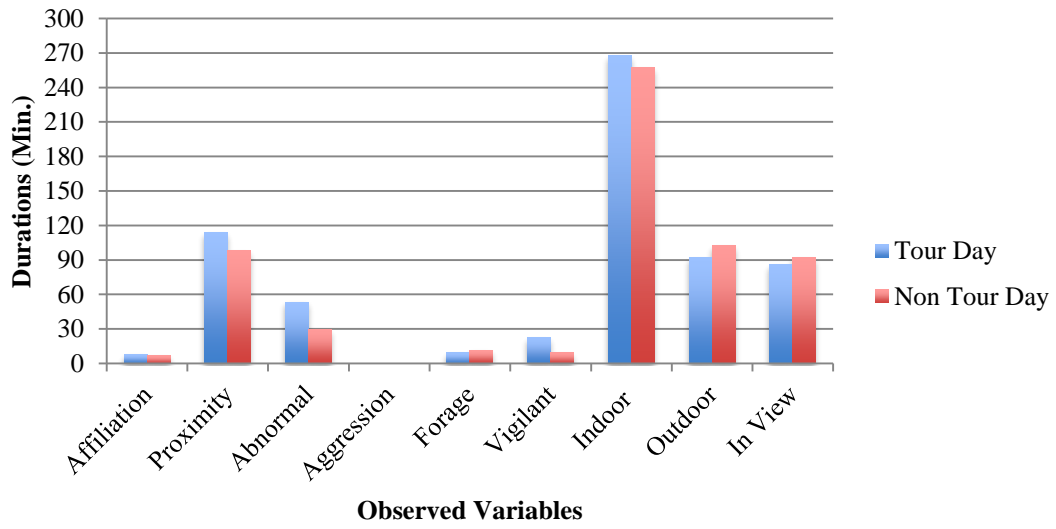
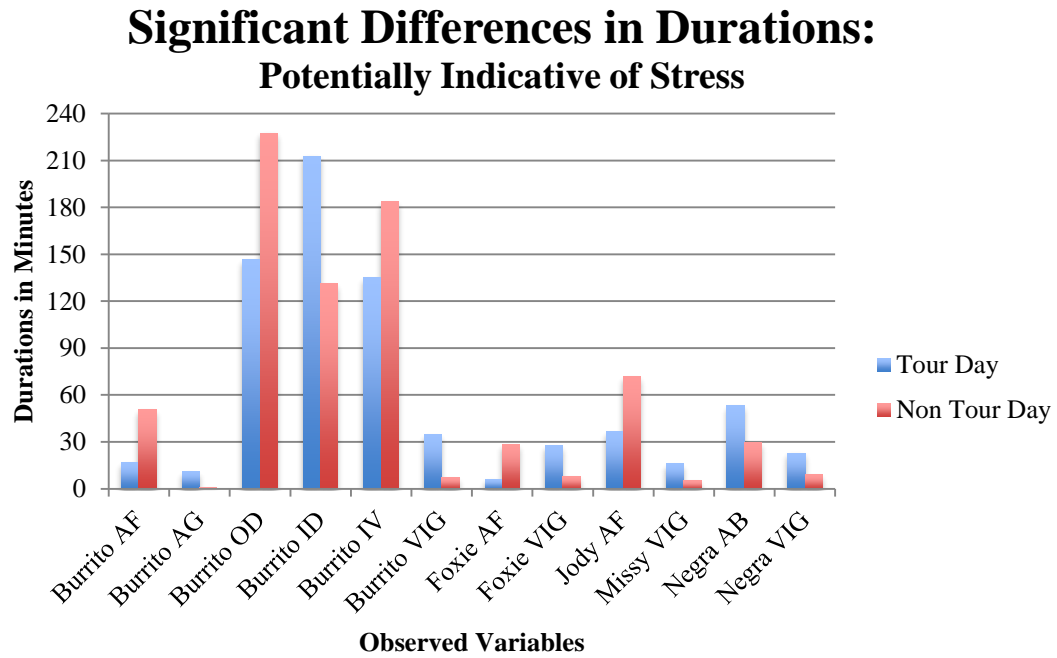


Figure C7. Negra's observed durations

APPENDIX D

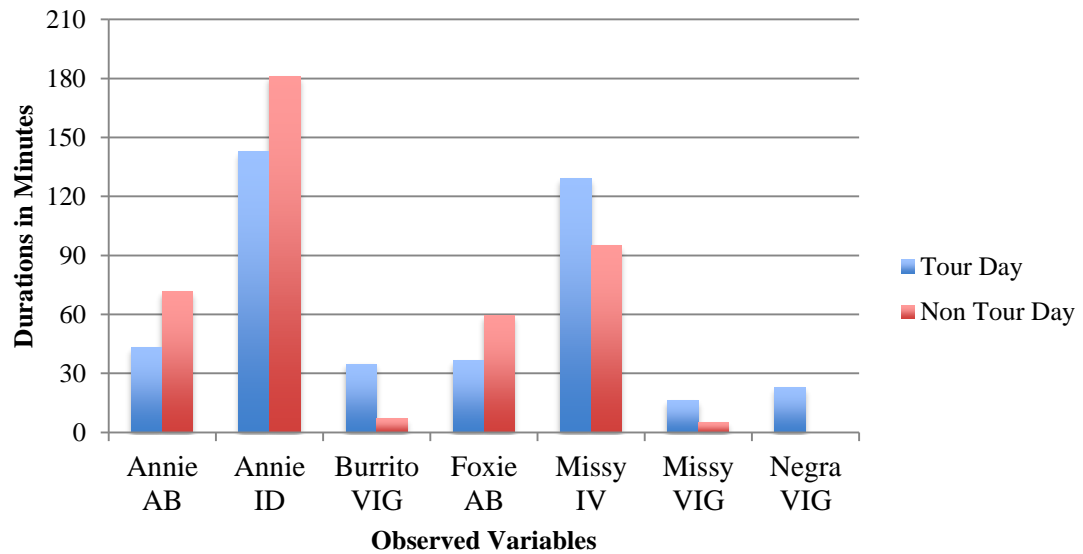
Graphs of Significant Differences in Combined Chimpanzees' Durations



Notes. AF = Affiliation, AG = Aggression, OD = Outdoor, ID = Indoor, IV = In view of visitors, VIG = Vigilant, AB = Abnormal

Figure D1. Significant differences in durations potentially indicative of stress

Significant Differences in Durations: Potentially Indicative of Enrichment



Notes. AB = Abnormal, ID = Indoor, VIG = Vigilance, IV = In view of visitors

Figure D2. Significant differences in durations potentially indicative of enrichment