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Monitoring Welfare in Captive Chimpanzees (Pan Troglodytes) Using Individual Positional Behavior and Substrate Use Profiles

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MONITORING WELFARE IN CAPTIVE CHIMPANZEES (PAN TROGLODYTES) USING INDIVIDUAL POSITIONAL BEHAVIOR AND SUBSTRATE USE PROFILES

by

Joey Lara

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ABSTRACT

MONITORING WELFARE IN CAPTIVE CHIMPANZEES (PAN TROGLODYTES) USING INDIVIDUAL POSITIONAL BEHAVIOR AND SUBSTRATE USE PROFILES

by

Joey Lara

The University of Wisconsin-Milwaukee, 2023
Under the Supervision of Professor Emily R. Middleton

The welfare of captive chimpanzees partly depends on the structural features present in their enclosure. An individual's manner of expressing positional behaviors depends on these environmental characteristics and may be reflective of their physical and mental health. This thesis seeks to further the scientific understanding of the relationships between positional behavior, substrate use and captive chimpanzee welfare. In pursuit of this goal, I designed and installed a novel vertical climbing aid onto a climbable platform structure within an enclosure at the chimpanzee sanctuary, Chimp Haven, in an effort to encourage mobility and vertical space use in the enclosure's residents. Additionally, I assessed the chimpanzees' tendencies for engaging in positional behaviors and using present substrates and enclosure areas. Finally, I examined the associations between particular substrates and the expressions of positional behaviors. The vertical climbing aid's effectiveness was assessed by reviewing video recordings of the two platform structures within the enclosure before and after the installation. Positional behavior and substrate use data were recorded for each subject via focal animal scan sampling.

The novel climbing aid was not effective during the study's duration. Occupation rates and elevation level change frequencies decreased on the experimental structure. Alternative approaches should be taken to future structural modification designs, implementations, and assessments. Individuals demonstrated unique profiles of positional behaviors and substrate use tendencies. The detailed positional behavior profiles and diversity could be useful in assessing and promoting physical health and welfare once validated with established welfare measures and medical records. Substrate use profiles and diversity metrics could similarly be used to determine the degree to which individuals avoid or are receptive to various stimuli. Hence, changes to substrate use profiles can be monitored to assess progress in efforts to encourage individuals to embrace diverse experiences as is the goal of provisioning enrichment. Finally, the associations between substrate use and positional behavior expression may be used to direct changes to enclosures based on the needs of its residents. Deficiencies in positional behaviors for a given chimpanzee may be addressed through the addition of substrates that are most associated with a desired positional behavior. This preliminary study outlines a new approach to measuring welfare as a function of positional behavior expression and environmental interactions. Future refinements to these methods are expected to contribute to the ability of captive management programs to infer a more complete understanding of the overall conditions of captive chimpanzees. Issues that impede a chimpanzee's wellbeing may then be addressed with suitable captive management strategies and the informed installation of appropriate substrates to improve welfare.

To the ape lineages that did not make it

through the Miocene Epoch.

You are not forgotten.

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I would first like to declare my appreciation for the chimpanzees that served as the subjects for this study: Apache, Cliff, Coco Nut, Dino, Fancy, Gary, Jake, Jane Austen, Maggie, Novella, PeeWee, Shone, Simpson, and Zort. I hope you all and any other chimpanzees who occupied the C200 corral have enjoyed the structural addition.

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Chapter 1: Introduction

1.1 Overview

Managing animals in captivity while effectively prioritizing their ethical treatment is a monumental task. The difficulty that some species experience under intensive human management has been inferred from a variety of metrics (Wolfensohn et al. 2018). This phenomenon is especially apparent for animals with expansive natural home ranges and daily travel distances (Clubb and Mason 2003; Kroshko et al. 2016) as well as those living in enclosures that lack appropriate environmental complexity (Abou-Ismail et al. 2010; Hoehfurtner et al. 2021; Sha et al. 2016). Despite their general adaptability, many primates are particularly vulnerable to the negative impacts of captivity (Hau and Schapiro 2007). Among the issues that arise in captivity are the variable limitations of the physical environment, which result in constraints to captive primate behavior that are largely absent in a given taxon's historic ecosystem (as in Ross et al. 2009). While humans praise our own ingenuity that enables the captive holding of many animals, it is beyond our limitations to recreate the complexity that exists in the natural environments in which these animals have evolved. It is similarly impossible to predict the effects on the wellbeing and development of an animal from the individual's interactions with the totality of the different aspects of their environment. Human controlled environments can only approach, to varying degrees of success, the inclusion of the total assortment of beneficial spatial, mechanical, and chemical structures present in the species' historic ecosystems (Vereecke et al. 2011).

Importantly, while a greater amount of available space can be beneficial for certain animals, these benefits may not be fully realized when captive animals fail to expand their space use throughout the entirety of their enclosure (Duncan et al. 2022; Ross et al. 2010). This tendency could be reflective of limitations of the physical environment, management and husbandry practices, or the presence of other sources of psychological distress (Ross et al. 2010). While naturalistic substrates are generally beneficial to captive primates' expression of species typical behaviors (Ross et al. 2011), the early life experiences and rearing conditions of animals can affect their comfort or stress levels when confronted with less familiar substrates even when they are more naturalistic and offer greater environmental complexity (Morimura and Mori 2010).

Like other apes, chimpanzees (*Pan troglodytes*) evolved to engage in a variety of positional behaviors in complex environments while relying on immediate and long-distance spatial awareness for foraging and survival (Potts 2004). Many of the skills required for chimpanzees' interactions with their environments, including tool use and arboreal acrobatics, are learned during their prolonged development periods via cultural transmission and long-term repetition and experimentation (Street et al. 2017). Without early life experiences that include long-term use of more naturalistic substrates in complex environments, the benefits of larger and more complex enclosures could be dampened (Duncan et al. 2022).

Facilities like Chimp Haven, the chimpanzee sanctuary at which the present study took place, represent the growing movement in animal care practices toward prioritizing animal welfare. At the time of this publication, there are around 330 chimpanzees currently housed at Chimp Haven (ChimpHaven.org). Many of the residents at the sanctuary are retired laboratory subjects from biomedical research (Reardon 2015). Most of these individuals have spent all or nearly all of their lives in captive settings and have no to little familiarity with the ecosystems within their species' historical distribution. The demographics of the population at Chimp Haven continue to grow more geriatric, and mobility issues can be expected to be more pronounced (Hopper et al. 2022; Neal-Webb et al. 2020). Subjective scoring of chimpanzee mobility by trained and familiar observers has been useful in assessing chimpanzee welfare (Hopper et al. 2022), and the pursuit of improving mobility may be an effective fulcrum for overall physical and mental welfare (Neal-Webb et al. 2020). Given the promising nature of this approach, it may be beneficial to expand on the use of positional behavior data as a welfare assessment tool and means of informing captive management practices.

Such a focus on examining locomotion in pursuit of greater welfare may present problems similar to those experienced during biomechanical locomotion research. Detailed studies on locomotion kinematics tend to be performed in simplistic and spatially limited captive environments using video footage and/or pressure sensors (Demes et al. 2015; Holowka et al. 2017; O'Neill et al. 2015; Samuel et al. 2018; Schoonaert et al. 2016; Sockol et al. 2007; Vereecke et al. 2011). Such conditions are not always feasible for regular individual assessment, particularly when one also prioritizes implementing environmental complexity for its enrichment value. Because chimpanzees tend to spend the majority of their time in stationary postures (Hunt 1992; Sarringhaus 2014), I suggest that physiological indicators of welfare may be more apparent when considering individual differences in detailed posture engagement tendencies, which can be collected even when a subject is stationary.

Given the departure of human-built structures and spaces from typical chimpanzee environments, a consideration of positional behavior and substrate use in wild chimpanzees could be used to inform the designs of enclosures and the structures therein to provide effective enrichment and mobility benefits to captive chimpanzees. Observed positional behavior and substrate use tendencies could in turn be used to assess and inform the design of enclosures.

My research contained two complimentary components. For the first component, I designed and installed a novel climbing aid onto a climbing structure within an enclosure at Chimp Haven. I reported data on the chimpanzees' use of the enclosure's climbing structures before and after the climbing aid's installation. For the study's second component, I observed positional behavior and substrate use of the chimpanzees occupying this enclosure in order to develop a method for assessing welfare based upon positional behavior expression and environmental interactions.

1.2 Goals and Hypotheses

The goal of this thesis is to further the scientific understanding of the roles that positional behavior and substrate use play in captive chimpanzee welfare. In pursuit of this goal, I tested the following four hypotheses (a summary is provided in Table 1.1).

Hypothesis 1:

Introducing the novel vertical climbing aid onto the platform structure will increase the frequency of climbing behaviors and the rates at which the enclosure's resident chimpanzees occupy the modified platform structure.

Rationale:

In wild contexts, chimpanzees tend to prefer the use of thinner diameter supports that permit the creation of frictional forces necessary to climb upon and maintain a body's attachment to the substrate (Cartmill 1979; Hunt 1992). Such substrates are employed less frequently in captive settings in favor of more stable, large diameter substrates that are capable of supporting

Table 1.1 Study Hypotheses and Rationales

	Hyposthesis	Rationale
1	Introducing the novel vertical climbing aid will increase the frequency of climbing behaviors and the rates at which chimpanzees occupy the modified platform structure.	The climbing aid was designed to permit the generation of frictional forces between the chimpanzee and the substrate with greater ease. Thereby, climbing on the modified structure would be safer and less energetically expensive. Assuming safety and energetic cost are factors that inhibit climbing frequency in chimpanzees, the climbing aid would effectively increase access to elevated spaces in an enclosure.
2	Captive chimpanzees display significant individual differences in their expressions of positional behaviors.	Chimpanzee behavior is known to vary by individual due to genetics, demographics, personality, skeletal morphology, social position, external conditions during critical developmental periods, and the experience of impactful short and long-term external events. Available evidence suggests that certain locomotor and postural behaviors vary significantly in type and frequency in both wild and captive chimpanzees
3	Captive chimpanzees display significant individual differences in their use of available substrates and areas of their enclosure.	Chimpanzee behavior is known to vary by individual due to genetics, demographics, personality, skeletal morphology, social position, external conditions during critical developmental periods, and the experience of impactful short and long-term external events. The immediate availability of and one's experience with features of an enclosure are known to impact the likelihood of chimpanzees' choices to occupy a given enclosure area.
4	Positional behavior expression correlates with substrate type, such that certain modes of locomotion and certain postures are expressed with greater frequency on particular substrates.	The expression of positional behaviors is characterized by interactions between the body and its surroundings. Different substrates have different forms and mechanical properties that would permit to varying degrees the expression of recognized modes of chimpanzee positional behaviors.

the weights of large climbing structures and the chimpanzees that climb on them (Brando and Coe 2022). The climbing aid was designed to address this potential impediment to creating frictional forces while climbing vertically on the supporting columns of an enclosure's climbing structure. An effective climbing aid would result in climbing that is safer and less energetically expensive. Assuming that these factors impede climbing frequencies and vertical space use in captive chimpanzees, the climbing aid should provide the chimpanzees with an effectively greater ability to access to the elevated areas of their enclosure. Making vertical space use more accessible may help to promote captive welfare as some captive chimpanzee groups show a preference for occupying higher elevations (Jensvold et al. 2001).

Hypothesis 2:

Captive chimpanzees display significant individual differences in their expressions of positional behaviors.

Rationale:

Chimpanzees are known to be variable in their individual behavioral expressions and personalities (Hopper et al. 2014; Massen et al. 2013; Pederson et al. 2005). This combined with individual differences in skeletal morphology due to genetic, demographic, and environmental factors (Huseynov et al. 2017; Smith et al. 2015; Zihlman et al. 2008) may be expected to produce conditions for individuals to express different positional behaviors at different rates. Individuality in positional behavior expression has been reported to some degree in the wild (as in Sarringhaus 2013), and in captivity (Sockol et al. 2007). Individual differences in positional behavior expression may be exaggerated in captive populations due to their varied ancestral provenience, human-influenced breeding practices, differential abilities to express particular positional behaviors in enclosures containing different naturalistic and non-naturalistic features, unique early life events and rearing conditions, ability to engage in typical learned behaviors during critical developmental periods, and the potential for differing social and cultural contexts to impact positional behavioral expression.

Hypothesis 3:

Captive chimpanzees display significant individual differences in their use of available substrates and areas of their enclosure.

Rationale:

As is the case for the expected individual differences in positional behavior expression, differences in demographics, skeletal morphology, and personality may be expected to influence the rates at which individual chimpanzees use particular substrates. Substrate preference and enclosure use in adults may be especially impacted by the long-term presence of available enclosure features, particularly during the infant and juvenile periods of their development (Duncan et al. 2022; Morimura and Mori 2010). Captive chimpanzees raised in the absence of their mother may fail to develop certain typical behaviors and appropriate environmental interaction (Spezio et al. 2021), potentially including familiarity with how a substrate is used such that their comfort with interacting with it is hindered (Morimura and Mori 2010). Similarly, failure to familiarize oneself with different substrates during juvenile play may affect their learned ability to interact with the substrate (Berghänel et al. 2015; Palagi and Cordoni 2012). Within a group, differences in personality affect the reactions of a chimpanzee to novel stimuli (Bateson and Nettle 2015; Hopper et al. 2014; Massen et al. 2013), so even under similar rearing and environmental conditions differences in space use and substrate composition, chimpanzees will choose to engage with substrates at different rates. Additionally, the limits to substrate availability in a given environment may lead to the monopolization of their use by particular individuals (Bettinger et al. 1994; Ross et al. 2009). Finally, individual morphological characteristics (Zihlman et al. 2008) may impact the physical comfort or energetic efficiency associated with locomotor modes and holding one’s body in specific postures.

Hypothesis 4:

Positional behavior expression correlates with substrate type, such that certain modes of locomotion and certain postures are expressed with greater frequency on particular substrates.

Rationale:

Positional behaviors constitute the means by which individuals interact with the substrates in their environment (Bezanson 2017). The morphological and mechanical properties of different substrates limit the ways that a chimpanzee can easily engage in different postures and locomotion types. For example, to engage in suspensory behaviors, a chimpanzee must interact with a substrate from which they can suspend. Quadrupedal walking requires a substrate form that can support the weight of the body exerted through the limbs at the points of contact with the substrate. Sitting requires a substrate to sit on, etc. This principle provides the basis for this study's attempt to catalogue the positional behaviors most likely to be expressed on the particular substrates available to captive chimpanzees.

I seek to use this thesis to present the applicable contexts and degree to which the high level of specificity in body element engagement type that I recorded in this study can be useful for analyzing mobility and physiological welfare. I will explore the potential for comparing posture and substrate use between individuals and groups in order to identify and address physiological and behavioral limitations among captive chimpanzees.

Based on the data reported in this thesis, I will propose any recommended changes to the structural makeup of the study enclosure as well as possible changes to behavioral management practices that could enhance the welfare of the study subjects. I hope to provide a jumping off point for expanding the framework for studying substrate use and positional behavior as outlined in this thesis, with the ultimate goal of identifying the likely effects on locomotion and postures from introducing particular substrates and substrate forms. I intend for the findings from this thesis, and any potential expansions on its themes, to be useful for those who manage captive ape populations and aim to modify environments and practices in order to encourage positive physiological and mental/emotional welfare in captivity.

1.3 Thesis Outline

In Chapter 2 of this thesis, I discuss the different approaches and metrics used under the growing paradigm of prioritizing the improvement of animal welfare in the management of captive populations. This situates the present study's focus on positional behavior, substrate use, and environmental design as ways to target the factors that influence the emotional states of captive chimpanzees. I review the academic literature on chimpanzee positional behavior and substrate use that informed the methodology employed in the present study and the design of the novel climbing aid that was implemented therein.

Chapter 3 outlines the study site and study population observed for this report. I provide the rationale for the design of the novel climbing aid and describe its construction and installation. I lay out the study design, including the ethogram and methodology used to collect positional behavior data on focal individuals, as well as the methodology used to record focal area data on platform structure use. I close Chapter 3 by describing the types of data categorization, analysis, and metrics that were used to assess positional behavior.

In Chapter 4, I present the results of this study. This includes the comparative frequencies at which the chimpanzees used the climbable platform structure prior to and after the installation of the vertical climbing aid. Results from positional behavior data analysis provide links between individual chimpanzees, substrate use, and positional behavior expression with a focus on limb engagement. Additionally, I present the calculated diversity indices for the engagement in positional behaviors, substrate use, and limb engagement under different classification schemas.

Chapter 5 provides a discussion of the implications of this research. I assess the efficacy of the vertical climbing aid in order to determine if it should be more widely implemented, or if a different approach to substrate design should be taken. I examine the positional behavior, and substrate use tendencies in different chimpanzees in order to identify the trends and limitations of individuals' positional behavior and interactions with their environment. Using these results, I describe how one could make recommendations for behavioral interventions and the installation of particular environmental structural enrichment with the goal of ameliorating or reversing any possible physical, mental, or emotional decline in these and other chimpanzees. Finally, I discuss the potential applications of this study's framework for promoting captive animal welfare, including the future directions in which to focus efforts to improve enrichment designs and means of assessing welfare in order to enhance the lives and wellbeing of captive chimpanzees.

Chapter 6 closes this thesis with an overview of the study, its conclusions, and the importance of continuing to implement new types of structural enrichment and further developing positional behavior based welfare metrics.

Chapter 2: Background

2.1 Major Approaches to Welfare Assessment and Promotion

The burgeoning field of animal welfare science encompasses many disparate approaches and analytical methods for assessing an individual's wellbeing, improving their living conditions, and identifying the factors contributing to both negative and positive emotional states (Robinson and Weiss 2023). The rightful prioritization of particular approaches may vary depending on the target species, individual, situational context, and the animals' immediate concerns (Mason 2010; Wolfensohn et al. 2018). However, because so many aspects of captive animals' lives are under human control, ideal practices toward promoting welfare involve a holistic consideration of the multitude of interrelated factors understood to impact animal welfare (Mellor 2016; Wolfensohn et al. 2018).

2.1.1 Physical Health Measures

Physical health measurements constitute a number of the commonly used means of inferring animal welfare (Veasey 2017). Greater overall health and longevity are thought to indicate the satiation of mental and physical needs, while earlier morbidity may be the result of negative affective states and the root causes of these internal experiences (Pressman and Cohen 2005; Walker et al. 2023). Animal management programs will use health measures like weight, blood pressure, heart rate, and notable pathologies to determine the need for life-sustaining medical intervention (Bonnichsen et al. 2005; Capitanio et al. 2023; Cole et al. 2020; D'eath et al. 2009; Doyle et al. 2008; Veasey 2017). These are also used to infer the presence of experienced stresses that diminish the ability of an animal's body to sustain optimum health (Walker et al. 2023; Weiss et al. 2011). Chronic stress can lead to a number of issues including a suppressed immune system, tissue inflammation, tissue damage caused by oxidative stress, longer recovery times from injuries, accelerated telomere shortening, and the earlier onset of the characteristics of older age (Archie 2013; Bateson 2016; Bateson and Poirier 2019; Hänsel et el. 2010; Obanda et al. 2014; Walker et al. 2023; Webster et al. 2002). When observed, the prevalence of these issues would suggest a high possibility that an animal is experiencing stress related to poor welfare. Moreover, the symptoms of deteriorating health caused by poor welfare can lead to further suffering and a lessened ability to deal with future adversity in a positive feedback loop of negative welfare (Neal Webb et al. 2019; Nunamaker et al. 2012).

Nutritional fulfillment is another important factor to consider when promoting physiological health. Captive programs may fail to provide feeding regimes that encompass the complex nutritional requirements fulfilled by wild diets under ideal conditions, resulting in poorer physical health (Caravaggi et al. 2018; Junge et al. 2000; Moittié 2022). This could also lead to changes in food and nutrient motivated behaviors (Britt et al. 2015; Masi 2011). Analyses of the microbiomes of primates living under more intense human control reveal the presence of gut microbiomes that converge more closely with those of humans, possibly due in part to the common elements of the nutritional profiles of humans and the animals that they feed (Clayton 2016). The adverse health impacts of particular nutrient deficiencies can be measured to ensure that basic biological and dietary needs are met. If nutritional needs are not met, one may presume the presence of internal states of suffering that serve as evolutionary adaptations to motivate behaviors related to eliminating the nutritional deficiency.

Overall lifespan is often used as a measure for assessing if a species or individual is able to thrive in captivity (Clubb et al. 2008). If health needs are not met or stress is prominent and chronic, individuals may have shortened lifespans compared to their wild counterparts that do not experience the same limitations on their health (Walker et al. 2012). High incidence of cardiovascular disease has been extensively reported on in captive chimpanzees, particularly as a result of interstitial myocardial fibrosis (Lammey et al. 2008; Nunamaker et al. 2012; Varki et al. 2009). Myocardial fibrosis is less prevalent as a cause of death in chimpanzees living in their species-historic contexts, although this topic requires further investigation (Strong et al. 2020). A recent report on the cardiovascular health of chimpanzees living in a more wild context have shown the absence of indicators of many other types of heart diseases (Cole et al. 2020). This suggests the need to identify and rectify the sources of the propensity toward cardiovascular disease in captive chimpanzees. The development of practices to improve the overall health of captive chimpanzees, particularly those related to cardiovascular disease, would likely be a prerequisite for achieving their maximum possible welfare.

2.1.2 Stress-Related Hormones and Immunity Signifiers

One of the most trusted avenues for assessing welfare is based on the theoretical understanding that states of suffering and distress are the products of hormonal regulation within an animal’s body (Capitanio et al. 2023). Hormones and other factors that are associated with common internal states and experiences in many animals can be measured quantitatively to provide sensitive measures of internal states related to negative and positive welfare (Capitanio et al. 2023).

The most common hormonal investigations involve measuring glucocorticoid production as an indicator of hypothalamic-pituitary-adrenal axis activity (Anestis 2009; Heintz et al. 2011; Otovic and Hutchinson 2015; Palme 2019; Yamanashi et al. 2013). Concentrations of glucocorticoids and their metabolites in animals are associated with the experience of stress (Touma and Palme 2005). For primates, the most abundant and useful glucocorticoid to measure is cortisol (Palme et al. 2005). One can invasively collect blood or saliva samples to analyze for cortisol concentrations, or measure cortisol concentrations in non-invasively collected urine, feces, hair, or saliva (Behringer and Deschner 2017; Heistermann 2010; Palme 2019). Similarly, epinephrine and norepinephrine concentrations can signify activation of the sympathetic nervous system as another indicator of stress (Capitanio et al. 2023). Concentrations of these two hormones are more sensitive to short-term experiences of stress and may be collected via blood draws or noninvasive urine collection. However, changes to the concentrations of these hormones over short periods of time make the measures less feasible as results are impacted by the events immediately preceding collection (Capitanio et al. 2023; Moberg 2000; Otovic and Hutchinson 2015).

Researchers and captive management programs may also measure immune function as an indicator of both physiological and psychological wellbeing (Hänsel et al. 2010; Staley et al. 2018; Walker et al. 2012). Experience of stress can alter immune functioning in several measurable ways, including antibody responses and changes to cytokine production (Capitanio et al. 2023; Hänsel et al. 2010; Yang et al. 2017). Measuring these immune functions requires invasive blood drawing, which could be stressful to captive primates (Capitanio et al. 2023; Heistermann 2010). Other biomarkers of inflammation may be measured from non-invasively collected urine sample, including neopterin, a compound produced as a byproduct of immunity-related cytokine presence, and C-reactive protein, which directs immune responses toward infectious agents (Heistermann and Higham 2015; Lamperez and Rowell 2005; Du Clos 2000)

While most hormone measurements have focused on collecting indicators of stress, other approaches involve measuring the concentrations of hormones that indicate positive welfare states. Dehydroepiandrosterone (DHEA) is a steroid hormone that can function to inhibit the effects of glucocorticoids (Whitham 2020). Some have suggested the use of the ratio of DHEA to glucocorticoids as a more effective measure of overall welfare as it affects the hypothalamic-pituitary-adrenal axis (Whitham 2020). Recent studies have also shown that urinary oxytocin, a hormone related to experiencing social bonds, can be effectively measured and may indicate a degree of social fulfillment (Leeds et al. 2023).

Hormone concentrations have a long history of use to infer welfare, but their effectiveness is not absolute. In many cases, the interaction between stressful experiences and hormonal indicators fails to follow predictable patterns. Known stressful events may fail to elicit increases to corticosteroid concentrations, and corticosteroid concentrations may rise in the absence of observable stressful events (Novak et al. 2013; Otovic and Hutchinson 2015). In fact, highly motivated positive affective states and activities associated with greater physical health, like sexual arousal, frequent exercise, and hunting actions can all cause increases in cortisol concentrations (Dawkins 2006). The presence of low glucocorticoid levels during stressful situations may be the result of acclimatization to present stressors, or reduced cortisol responses as a result of chronic stress (Romero 2004). Moreover, it can be difficult to standardize collection methods for hormone levels, as the time of collection, and even point of origin on the body can have an impact on the concentration and deposition of target hormones within a tissue (Otovic and Hutchinson 2015).

Despite the many complicating factors and shortcomings of analyzing hormonal indicators of stress and welfare, this practice remains one of the primary metrics employed by researchers to assess the internal states of animals with a relatively high level of reliability. This may be in part because the quantitative results of these tests facilitate sensitive mathematical comparisons that, even if they do not perfectly coincide with welfare, offer the promise of future refinement that could ultimately yield biochemical analyses that offer accurate assessments of animals' internal states.

2.1.3 Behavioral Indicators of Welfare

The internal mental and emotional states of animals can translate into outward observable behaviors. These are particularly apparent in more social animals like most primates, who have evolved to display signals of their emotional states to other individuals (Parr and Waller 2006). Experienced human caretakers can interpret the meanings behind some chimpanzee facial expressions, and some researchers have suggested using facial recognition software to interpret facial micro expressions (Descovich et al. 2017). Changes to non-socially directed behaviors are also apparent as a response to internal states (Lutz and Baker 2023). By recording the frequencies of an animal's behaviors, caregivers and researchers can compare their expression within a species and infer the internal states associated with behavioral motifs (Lutz and Baker 2023).

Behavioral indicators of negative welfare can elicit the most visceral assessments of animal welfare by observers. Many wild species held in captivity are known to exhibit abnormal and stereotypic behaviors that are rarely seen in their wild conspecifics (Birkett and Newton-Fisher 2011). Stereotypies may include repetitive abnormal behaviors or typical behaviors expressed in an extreme and repeating manner outside of their typical context (Mason 1991). Abnormal and stereotypic actions are thought to serve no practical biological function outside of their role as immediate stress outlets (Garner 2005). In extreme cases, these actions escalate to self-injurious behavior, which can lead to wounds that contribute to suffering and may even result in death (Dorey et al. 2009; Pizzutto et al. 2015; Skyner et al. 2004). Such maladaptations signal captive conditions that diverge so acutely from those that an animal has evolved to navigate that responses to averse stimuli are inappropriately formed and directed.

Other behavioral indicators of stress may be expressed throughout the typical course of life for a species in its historically occupied locales. However, their rates of expression can be used to infer welfare and may be abnormally high in chronically stressed captive animals (Baker and Aureli 1997; Reamer et al. 2010; Vick and Paukner 2010). Chimpanzees in captivity can exhibit a number of abnormal, stereotypic, and self-injurious behaviors including but not limited to: pacing, coprophagy, urine drinking, fecal manipulation, rocking, trichotillomania (excessive hair pulling that leads to hair loss), excessive self-scratching, regurgitation/reingestion of food, spitting, clapping, self-hitting, self-biting, hitting one's body against a surface, eye poking, body jerking, shaking, wound-picking, head tossing, and incest (Birkett and Newton-Fisher 2011). Those charged with assessing the welfare of captive chimpanzees can record frequencies of these behaviors and track their changes over time while implementing efforts aimed at diminishing their expression. Wounds and noticeable appearance changes that result from self-directed actions can be recorded asynchronously to the injury producing incident (Ross et al. 2009). In chimpanzees, wounds also commonly emerge from violent agonistic social interactions (Ross et al. 2009). Chimpanzees, like most primates, are highly social and seem to place great importance on the relationships with other members in their group (Samuni et al. 2018). Navigating social and power hierarchies can be complex and stressful as it is difficult for one to assess the future consequences of social decisions and alliance networking (Ramos-Fernandez et al. 2018; Seyfarth and Cheney2015; Watts 2006). When violent conflicts are more frequent, individuals are likely to experience greater levels of stress and anxiety (Yamanashi et al. 2016).

Given the importance of sociality in chimpanzees and the potential for stress and injury related welfare detriments that can result from fights, welfare focused captive management programs monitor social turmoil and seek to reduce instances of aggression. Intra-group conflicts can arise from other underlying issues of heightened anxiety and irritability that increase individuals' propensity for violence (Yamanashi et al. 2016). Therefore, the frequency of agonistic behaviors can signify the overall relative stress experienced by a group, not just the factors innate to social dynamics (Whitehouse et al. 2013; Yamanashi et al. 2016). This is evolutionarily sensible as times of periodic ecological insecurity lead to a greater need for individuals to compete for access to the more limited resources that are available to their group. As conflicts can escalate to violence from less severe antagonistic or non-prosocial interactions, other signals of brewing conflicts are also used to understand a chimpanzee's social stress. These signals include teeth baring, fear grimacing, high rates of positional displacement, individual avoidance, rejecting others' attempts to make social contact, and bluff displays (Baker and Aureli 1997; Funkhouser et al. 2018). Noted changes to the frequencies of stress-related behaviors can be used in context with the preceding events to determine the causes of stress for an animal. Welfare focused care can then make informed changes to management practices to reduce stress.

Understanding the internal states of animals also requires an assessment of the desirable behavioral indicators of positive welfare that welfare-focused captive programs seek to promote. Monitoring positive behaviors can grant insight into a larger view of welfare that considers not just the absence of negative experiences but also the presence of positive affective states (Lutz and Baker 2011; Mellor 2015). One can assess the social dynamics in a chimpanzee group and its impact on welfare by quantifying occurrences of affiliative and prosocial behaviors. These include instances of allogrooming, greetings, proximity to other individuals, reassurance giving/ receiving, food or object sharing, partnered play, and sexual interactions (Pomerantz and Terkel 2009; Funkhouser et al. 2018; Yamanashi et al. 2018). Promoting these positive interactions can encourage the feeling of social connectedness that will improve the lives of these social animals and can develop the bonds that ameliorate social conflict (Duncan et al. 2013; Fraser et al. 2008; Shutt et al. 2007). Play behaviors, and the inference of an animal having fun, are similarly used to determine positive welfare (Held and Špinka 2011). Moreover, the expression of play behaviors is theorized to occur more often in mammals when they have access to sufficiently abundant resources (Burghardt 2014). This allows them to invest energy into the skill refinement purpose thought to motivate both solitary and social play behaviors (Špinka et al. 2001).

There are issues with relying exclusively on prosociality and playfulness as measurements of welfare. Prosocial behaviors can occur alongside aggression, and alliances can be deployed to initiate new conflicts with other chimpanzees (Enigk et al. 2020). Prosocial and play behaviors can both be employed to cope with stressful conditions at times (Judge et al. 2006; Tacconi and Palagi 2009; Nieuwenhuijsen and de Waal 1982; Videan and Fritz 2007). A group's ability to use these coping strategies signifies conditions sufficient enough to allow for a certain level of behavioral flexibility, but sudden increases in their deployment can signify the presence of underlying welfare issues. Therefore, it is preferable to consider the occurrences of prosocial and play behaviors within the animals' larger experiential context. Animal management programs can then develop practices to simultaneously minimize negative behavioral indicators and maximize positive behavioral indicators of welfare.

2.2.3 Behavioral Diversity

When multiple behaviors are measured to infer captive animal welfare, it may be advantageous to synthesize these frequencies into a single value. In recent years, behavioral diversity has been proposed as a potential metric for measuring welfare. Miller et al. (2020) suggested the use of the Shannon Diversity Index, originally conceived to quantify ecological diversity, to generate a diversity score for the expression of predefined behaviors in captive individuals (Shannon 1948). The rationale for considering diversity of behaviors comes from the recognition that poor welfare states are associated with a limited behavioral repertoire. Bouts of stereotypic behavior in captive animals are seen as antithetical to the expression of a myriad of behaviors in different contexts. A lack of behavioral diversity may also relate to disengagement with aspects of one's environment, a behavioral feature related to chronic depression and reward insensitivity (Proudfit et al. 2015). In captive animals, this could present as failure to engage with enriching stimuli and motivated behaviors. As is the case with stereotypic behaviors, negative internal states and coping mechanisms can create positive feedback loops that keep an individual locked into negative emotional states (Garner 2006). Individuals that do express a variety of behaviors may demonstrate a greater ability to modulate their actions and emotions depending on the situational context. If behavioral diversity could be encouraged, an animal may be less restricted to their familiar behaviors. The presence of other behavioral options, along with potential human caretaker intervention, could act as a form of behavioral interference and activation to prevent an individual from falling into cyclical negative emotional states. Furthermore, other efforts to improve welfare could be more effective for individuals that are behaviorally and emotionally responsive to their implementation in more appropriate manners.

However, as Cronin and Ross (2019) pointed out, there are several problems with the behavioral diversity approach to measuring welfare. They argue that such metrics are difficult to standardize and mathematically flawed. The predefined behavioral categories that are selected for these measurements are not necessarily comparable. Behavioral diversity scores are largely dependent on what categories of behaviors the researcher decides to break up into multiple behavioral categories. True behavioral diversity may be missed if it is expressed within the confines of a category that has not been split. Similarly, greater emphasis may be placed on certain types of behavior that may be more apparent to the human eye, but not necessarily more important for an animal and their beneficial behavioral expressions. Furthermore, observers must decide whether to include behaviors that are considered to be negative indicators of welfare. If these are included, then an individual who expresses a number of negative behaviors, even multiple stereotypic behaviors, could produce a high behavioral diversity score. If all negative behaviors are excluded, this introduces the problem of determining the positive or negative value of each behavior. Whether a behavior is actually indicative of negative welfare in all cases and for all individuals is not a certainty. Captive chimpanzees often exhibit certain abnormal behaviors more often than others (Birkett and Newton-Fisher 2011). A behavior could be healthy or neutral for one individual or in one context (e.g. self-scratching or self-directed picking in response to an environmental irritant) but could indicate or exacerbate stress in other contexts (e.g. self-scratching and skin picking as a stereotypic behavior) (Birkett and Newton-Fisher 2011). When these contexts are the internal states of the subject, it is even more unclear what value their expression holds.

Despite the complications that arise when using behavioral diversity as a welfare metric, Hall et al. (2021) demonstrated how these may be navigated to validate behavioral diversity indices as useful welfare metrics. They found that multiple indices of behavioral diversity using the Shannon Diversity Index were inversely correlated with higher concentrations of fecal glucocorticoid metabolites. Diversity scores that excluded negative behavioral indicators of welfare were correlated with reductions in stereotypic behaviors. The most effective index, which was inversely correlated with both glucocorticoid metabolites and stereotypic behaviors, excluded negative behaviors and split certain positive behaviors. While different behavioral diversity indices may be validated by other metrics with different degrees of efficacy, the issues with these metrics may be addressed by exploring the inclusion and exclusion of particular behaviors.

2.1.4 Subjective Evaluations

Subjective measures can also be employed by caretakers who are familiar with individual animals' behavioral ranges and readily recognize deviations from their normal behavior (Robinson et al. 2016). For these metrics, caretakers rate different aspects of the animals' behavior personality or inferred emotional states (Gartner and Weiss 2018; Robinson et al. 2016). While not as empirical or quantitative, this method can make use of the human brain's pattern recognition and empathetic abilities. Recently, there has been increased acceptance of the idea that many emotional states are common among different clades of animals (de Waal 2020). Given the importance of inferring the internal states of others within the evolutionary history of humans, we may rely to varying degrees on the inferences we make about other animals' minds based on our unconscious information gathering. For other primates and dogs in particular, our close genetic and social-evolutionary relationships permit these empathetic evaluations with greater reliability (Bloom and Friedman 2013; Graham and Hobaiter 2023). The relationships between caretakers and apes can be critical for understanding and addressing the captive subjects' needs.

2.1.5 Enrichment and Boredom

Another major welfare goal of captive programs is to provide a complex and stimulating environment (Kemp 2023). This is achieved by providing enrichment to the animals in order to prevent boredom and the negative emotional states with which it is associated (Meagher 2019). Some undesirable and stereotypic behaviors, like excessive self-grooming and hair loss, are thought to arise due to boredom and a lack of options to perform more purposeful actions (Beisner and Isbel 2008). Wild activity budgets for primates like chimpanzees are often characterized by large amounts of time dedicated to foraging and travel (Couturier et al. 2022; Inoue and Shimada 2020; Maurice et al. 2020). If the need for so much of one's time to be put towards these behaviors is reduced in captivity, primates' minds may be ill-prepared to occupy the remaining time available to them (Meagher 2019). Furthermore, as primates have evolved alongside the need to move through complex environments, manipulate certain aspects therein, and navigate difficult social situations, a lack of opportunity to apply their cognitive abilities in these ways may leave certain innate behavioral tendencies unfulfilled in inadequate environments (Hanson 2016; Neufuss 2017; Schmidt 2011). Enrichment provisioning is meant to both provide mental stimulation and to occupy the time of a captive animal (Kemp 2023). Feeding enrichment practices and devices can increase the amount of time an individual spends foraging and can provide a challenge for the animals to solve (Inoue and Shimada 2020). Enrichment may also involve providing manipulatable objects to play with, installing structures for individuals to climb on, and introducing a variety of tactile, olfactory, and acoustic sensory stimuli (Kemp 2023). If enrichment is sufficiently abundant and appropriate, an animal should have less uninterrupted time to experience negative emotional states and will sustain lower levels of distress from an unfulfilled need to process information. Another important component of ape enrichment in particular may be engaging in positive reinforcement training with caregivers (Claxton 2011; Fernandez 2022). These activities can provide a solvable challenge for the apes, facilitate positive interspecific social interactions, and help encourage behaviors that aid in the care of the animals (Laule and Whittaker 2007; Meehan and Mench 2007). Even without a challenging aspect, greater variety in the experiences of captive animals is thought to encourage engagement with their surroundings and the demonstration of different affinities for and behaviors associated with specific stimuli (Kemp 2023). This overall mental stimulation can lead to the positive affective states that welfare-focused programs seek to promote.

2.1.6 Choice and Freedom

Humans have control over much of the lives of captive animals. Because of this, captive management programs have the power to change captive conditions in pursuit of greater welfare in a way that the captive individuals are not able. However, there are limits to humans' understanding of what is best for a particular animal. A common function of animals' executive control and cognition is to weigh options and make decisions as to what is best for oneself, their fitness, and their experience towards the satisfaction of particular needs and goals (Ardila 2008; Jurado and Rosselli 2007). In recognizing this, those responsible for captive animal care can use an animal's innate abilities to seek out particular desired conditions and behavioral expressions to direct efforts towards improving the individual's welfare based on the animal's input in the form of collected behavioral data (Browning and Veit 2021).

In recent years, greater emphasis has been placed on the welfare value of allowing captive animals the ability to make decisions that have a significant impact on their experiences (Špinka 2019). The feeling of freedom is thought to be an important aspect of animals' contentedness (Schmidt 2015). A highly anthropogenically controlled setting negates one's ability to make impactful decisions. Even when humans make informed decisions for the provisioning of experiences to a captive animal, the individual may still experience distress from their inability to choose to perform a different action if it deems doing so appropriate (Schmidt 2015). A lack of input from an animal in crafting their experiences can lead to poor welfare and high anxiety as such an animal cannot predict the occurrence of events and exercise their will to avoid the potential for negative outcomes should they arise (Bassett et al. 2007). This can result in the animal experiencing higher degrees of distress and skittishness as their inability to effectively alter their behavior to address any potential negative outcomes is diminished. They may then operate on the assumption of negative outcomes and enter into a more extreme fight-or-flight state as a biological mechanism for dealing with unavoidable and undesirable experiences (Bethel et al. 2012). Animals have greater inferred welfare when given more impactful choices and more ability to choose their actions, social partners, and location (Clark et al. 2011; Neal Webb et al. 2020; Schapiro and Lambeth 2007). Today, common management practices involve making participation in events voluntary, but encouraged with rewards (Behringer et al. 2014). When given the choice of whether or not one engages with novel stimuli, the act of engaging is less distressing if the animals know they are able to flee the situation if necessary (Bassett and Buchanan-Smith 2007; Neal Webb et al. 2018). Even when the alternative option is not pursued, its presence can still have a behavioral impact on the individual (Kurtycz et al. 2013). This scenario may lead to an animal experiencing less anticipatory anxiety necessary to deal with the negative outcomes that they think could possibly arise as fleeing to more familiar surroundings remains an identifiable and applicable potential response (Lagisz et al. 2020).

If one allows for an animal to make choices for the experiences they wish to have, one can learn about an animal's individual desires. With this information, captive management programs can provide more preferred enrichment and experiences to the animals that may have a greater positive impact than the provision of enrichment that is not informed by individual preference (Kemp 2023).

Providing captive animals with decisions can not only benefit their wellbeing but can also be used to assess their mental state. When presented with a novel or ambiguous stimulus, an animal can exhibit behaviors that signify the expectation of negative, positive, or neutral outcomes (Pomerantz et al. 2012). By examining bias in the anticipatory states of animals, one can potentially interpret their outlook on the world as well as their amenability to changes aimed at further improving welfare (Lagisz et al. 2020).

While the choice approach to animal welfare is informative, it also has its limitations when applied on its own. Animals who are experiencing psychological distress do not always make choices that adequately address these issues (Franks 2019). In the case of stereotypic behaviors, an animal's coping actions can result in cyclical patterns of further distress and reliance on stereotypic behaviors (Mason 1991; Pizzutto et al. 2015). In a captive setting, certain behaviors that may be appealing to an animal could be present in such abundance that their selection to continually engage in these behaviors is deleterious to the individual's health (Learmonth 2019; Reamer et al. 2020). This can be seen in captive chimpanzees that may spend exaggerated amounts of time resting, occupying terrestrial contexts, or failing to utilize all aspects of their enclosures (Ross et al. 2011; Neal-Webb and Schapiro 2023; Ross et al. 2021; Yamanashi and Hayashi 2011). Stressed animals can have a tendency to choose the familiar and comforting, even if willful engagement in novel experiences would ultimately be more beneficial to their wellbeing (Wormald 2016). The unique early life experiences of chimpanzees can have a pronounced impact on whether the individual is able to make effective decisions to improve their quality of life (Bradshaw et al. 2008; Jacobson et al. 2017). Ultimately, the choices and immediate desires of captive animals are affected by the anthropogenic control over their lives, a situation that many animals may be evolutionarily unequipped to respond to with appropriate choices (Franks 2019). This phenomenon may be addressed by encouraging individuals to make more choices that result in positive outcomes in order to overcome negative mental biases and the inflated perceived odds of negative outcomes that limit an individual's perception of viable choices. While the outcomes of choice for individuals should be considered when caring for the animals, caretakers must also seek to expand the ability of individuals to make more impactful decisions.

2.1.7 Species-Typical Behavior Expression

A common thread in animal welfare science is to forefront the goal of encouraging the captive animals' expression of species-typical behaviors that are observed in wild conspecifics (Browning 2020). Prioritizing species-typical behaviors in captive animals provides a more appealing and accurate representation of animals for human viewing and likely also benefits the lives of the animals (Gaengler and Clum 2015). With some flexibility, present day animal species are understood to have evolved to exhibit behaviors that improve their fitness within the ecological niche they inhabit in their historically occupied ecosystems. When a clade has differentiated to rely on the expression of certain behaviors in particular proportions, it may develop physiological and mental adaptations that make these behaviors more effective toward improving fitness (Ferry-Graham 2002). Greater reliance on these behaviors over evolutionary time can make the clade dependent on their expression and the environmental features that facilitate their exhibition (Futuyama and Moreno 1988). If an animal's fitness is dependent on behavioral interactions with certain environmental contexts, their propensity to engage in such behaviors would operate on the assumption of the presence of appropriate environmental contexts. Even when basic living needs are met in captive settings, the propensity for these actions remains due to their history of evolutionary importance (Garner 2005). Negative welfare consequences then arise when an animal of such a species lacks the opportunity to engage in the behaviors that they seek to perform.

Species-typical behaviors occur in certain proportions in the wild that likely vary within an evolutionarily optimum window. In cases where these behaviors are expressed in captivity, they may not occur in species-typical proportions (Yamanashi and Hayashi 2011). An inability to perform behaviors in those proportions may cause distress as an evolutionary tool to seek the target equilibrium of behavioral expressions that optimizes the individual’s fitness (Garner 2005). When captive animals seek to alleviate their distress but are unable to take actions to do so in less appropriate environments, negative mental states persist along with the undesirable living conditions (Mason 1991). Stereotypic behaviors associated with stress are theorized to be an outlet for the displacement of energy and will to perform a behavior that is denied to an animal (Clubb and Mason 2007).

By considering the expression of species-typical behaviors in the wild, one can identify the normal propensity for behaviors that are carried out when conditions are less restrictive than in a human-designed environment. Welfare focused captive management programs may seek ways to encourage animals to emulate the expression and frequencies of species-typical behaviors (Lutz and Baker 2023). This could ensure that the captive animals express evolutionarily important behaviors in frequencies that fall into the ideal windows that preclude the need for distress and unsuccessful efforts to display behaviors in appropriate proportions.

This approach to welfare has garnered detractors for several major reasons. First, every behavior exhibited by an animal in less human controlled settings is not necessarily indicative of positive welfare (Learmonth 2019). Feelings of distress and anxiety ultimately have evolutionary origins and exist independent of an animal’s confinement by humans (Yeates 2018). Animals living in their species-historic ecosystems will experience distress and suffering during their lives even without human interference (Browning 2020). Some stress-related behaviors displayed in animals outside of human control are largely exhibited as responses to the presence of undesirable conditions and stimuli that affect or threaten to disrupt homeostasis (Clark et al. 1997; Moberg 2000). For example, actions motivated by a fear of predators indicate undesirable affective states (Mellor 2015b). Despite its natural occurrence, if a captive animal engaged in such a behavior in the absence of any predation risk, it would be both inappropriate for a situation and indicative of stress. Because captive management programs do have control and responsibility over so much of the associated animals' lives, they should try to ameliorate as much distress in the animals as possible, even if a certain amount of stress would exist outside of human control. Without investigations into the contexts in which certain behaviors occur, it is not necessarily clear which behaviors expressed in the wild are indicative of positive welfare. The species-typical behavior approach to welfare outlines a goal, but achieving it requires further understanding of the motivations for engaging versus not engaging in these behaviors. From there, behaviors that are beneficial and suggestive of welfare can be identified and encouraged in order to promote better captive living conditions.

2.1.8 Positional Behaviors and the Structural Environment

2.1.8.1 Evolutionary Background

The sources of negative welfare that are uniquely prevalent in captivity are ultimately derived from its defining quality: the degree of human planning and control over the environmental setting. The spatial confinement and human engineered structural makeup of enclosures are perhaps the most apparent features of anthropogenic environmental control.

Evolution has shaped the physiology and behavior of animals to sufficiently survive and reproduce within larger potential ecological contexts. For most animal clades, this means regular travel is necessary to meet the biological requirements to persist. Mobile animals vary in frequency, means, and distance of travel, as well as the structural and mechanical complexities of the collection of substrates they traverse (Granatosky 2018). Traveling to new locations is necessary to find food after a nutritional resource is depleted, to disperse in search of mates, to evade predators, and to avoid direct and indirect resource competition, (Bidner et al. 2018; Lee and Strier 2015; Trapanese et al. 2019). Most primates live in group units that occupy particular home ranges, within which constituents travel to procure available and preferred resources (Strier 2017). These resources may be sparsely distributed and temporally bound within their home ranges (Strier 2017). Many primates territorially exclude other groups from the area in order to maintain probable access to future bounties (Strier 2017).

Mobility and travel are important means for evolutionary success and functioning within complex ecosystems. Insufficient propensity to invest energy in travel would lead to deficient foraging, fewer opportunities to interact with potential mates, lower ability to evade predators, and failure to sustain membership in a group and benefit from the safety and resource security advantages that group living affords. While different species and primate groups may stay in one locale for less or greater durations, the ability to investigate alternative sites and leave their current one likely remains important in case conditions change.

A natural tendency towards changing one's spatial position over very short distances is also necessary to motivate the fulfillment of environmentally dependent needs. This tendency is also balanced against the energetic cost and potential rewards associated with such locomotion and posture engagement (Janson 2007). Primates may be especially dependent on a variety of positional abilities in order to move through a complex environment due to their arboreal evolutionary history (Granatoski 2020). The order Primates emerged and developed to navigate arboreal environments with erratic, non-uniform substrate makeups (Cartmill 1974). Primate evolution coincided with the emergence of angiosperms and their locomotor types have been hypothesized to have enabled the exploitation of fruit resources (Sussman et al. 2013). Primate physiologies reflect this, as they tend to be capable of employing a diverse set of positional behaviors that allow their traversal of a variety of substrates with different orientations and mechanical characteristics (Saunders et al. 2017).

Despite their arboreal origins, many primates can also or primarily employ terrestrial locomotion to reach desired destinations (Patel 2009). This is partly necessary because the global climatic changes that occurred throughout the Miocene Epoch led to more fragmented forests and a contraction of tropical forests to more equatorial zones (Potts 2004). Other derived locomotor adaptations for navigating beyond the limits of exclusive continuous arboreality have emerged across primate taxa, including long distance leaping, more efficient ground travel, high speed terrestrial sprinting, and swimming (Bismark 2010; Cannon and Leighton 1994; Graham and Socha 2020; Isbell et al. 1998; Patel 2009; Yeager 1991). Throughout the Miocene, apes especially developed large repertoires of positional behaviors to enable their continued exploitation of the diminishing, preferred just-ripe fruits (Hunt 2016). Most notable is the greater reliance on forelimb suspensory locomotion and postures, which are thought to enable more effective, safe, and sustained feeding on fruits residing on terminal tree branches (Almécija et al. 2021; Myatt and Thorpe 2011). This can be seen as an expansion of the positional behavioral repertoire for application within the most erratic substrate portion of the trees. Additionally, their lack of tails likely required apes' replacement of the balancing function of an arboreal tail with additional limb engagement styles. Still, the African apes are thought to have grown more reliant on terrestrial locomotion over time in order to more safely travel between desired arboreal resources, particularly when there are gaps in easily traversable branches between trees (Hunt

2016; Kivell and Schmitt 2009). Chimpanzees occupy a mixture of terrestrial and arboreal contexts. Typically, they will travel longer distances by terrestrial means but often forage and sleep in arboreal settings (Hunt 1992). The semi-arboreal semi-terrestrial chimpanzees and bonobos are able to utilize their broad positional behavioral repertoire to reach both preferred arboreal and terrestrial resources while balancing the predator risk characteristic of terrestriality and the falling risk characteristic of arboreality (Anderson 2018; Stewart and Pruetz 2013).

2.1.8.2 Welfare Impacts

Primates have evolved to be behaviorally dependent on mobility and travel as necessary prerequisites for their own fitness. As mentioned previously, welfare issues are thought to arise when an animal's ability to fulfill the natural drive to engage in these behaviors is denied by human captivity. Diminishing welfare may result from the incongruity between the internal or physiological need to engage in mobile behaviors and the practical limitations on actualizing the behaviors (Neal Webb et al. 2020). Efforts to promote species-typical behaviors should include considerations of the natural spatial and positional behaviors exhibited by conspecifics living in their species-historic ecosystems (Neal Webb and Schapiro 2023). For chimpanzee welfare, this means it is necessary to focus human efforts towards implementing environments, substrates, and management practices that are conducive to the expression of the broad set of spatial and positional behaviors of which chimpanzees are capable and typically utilize in their historic contexts.

Chimpanzees have been reported to occupy home ranges greater than 8.5 km^2 and even around 20 km^2 with daily travel distances of 2-4 km per day (Ross and Shender 2016; Vieira 2019). Human control over environments severely limits the ability for chimpanzees to occupy, travel through, and express control over their spatial position within such a large territory. While no enclosures reach the area of the natural territories of chimpanzees, enclosures can vary in size and their space-related impacts on the denizens. Currently, the National Institutes of Health (NIH) recommends chimpanzee enclosures contain 250 ft^2 per individual (NIH 2014).

Studies focused on the welfare impacts of introducing captive chimpanzees and other apes to more spacious enclosures with attention paid to space per individual have reported positive effects. Jensvold et al. (2001) found that introduction into a more spacious and complex enclosure led to chimpanzees expressing more species-typical behaviors with positional behavior expression within the range identified for wild conspecifics. Ross et al. (2011) similarly noted that a larger, more naturalistic enclosure had positive behavioral impacts on chimpanzees, including reductions in abnormal behaviors. Some have concluded that, while increasing the size of enclosures is beneficial to chimpanzees, these impacts diminish with ever-larger enclosure spaces (Appleby 1997; Neal Webb et al. 2018; Ross et al. 2011). While Neal Webb et al. (2018) found that absolute enclosure size increases resulted in the chimpanzees exhibiting more locomotor and behavioral diversity, they also showed that moving chimpanzees to a smaller enclosure with more usable vertical space similarly resulted in increased behavioral diversity. Notably, the smaller enclosure still met the NIH standards for minimum enclosure size. This highlights the need to provide enclosures not just with adequate absolute space, but also adequate amounts of effectively usable space.

The features present within an enclosure will impact the space use and the behaviors exhibited by captive animals (Honess and Marin 2006; Stoinski et al. 2001). Enclosure complexity has been proposed to be the prime means of improving environments that surpass a certain spatial threshold (Neal Webb et al. 2018; Ross et al. 2011). The abundance of structural enrichment as a part of this complexity is thought to produce positive mental and emotional effects by permitting greater variety of interactions with one's environment (AZA Ape TAG 2010). The overall design of enclosures and the features within can more effectively achieve this goal if designers consider how the residing animals will use these spaces (Brando and Coe 2022; Kemp 2023; Mallapur et al. 2005). Ross et al. (2009) found that more full utilization of space could be achieved when enclosure designs were informed by the space use characteristics of the chimpanzee and gorilla groups that were fated to reside in the new enclosures. In this case, space use was employed to signify the appropriateness of the enclosure.

By synthesizing the results of the aforementioned studies, it is apparent that enclosures with greater size, greater complexity, and greater attention paid to animals' actual use of space can all be used when designing enclosures in order to encourage behavioral outcomes associated with positive welfare. With further attention paid to the behaviors that are characteristic of interactions between chimpanzees and particular features of their environments, captive management programs can design more usable enclosures that more effectively enhance captive welfare (Ross et al. 2009).

Mobility, activity and overall physical fitness are important factors for primate health and wellbeing that are dependent on the spatial and structural characteristics of the subjects' surroundings (Caws et al. 2008; Jensvold et al. 2001; Neal Webb and Schapiro 2023; Neal Webb et al. 2018; Neal Webb et al. 2020). Given that positional behaviors are the means by which an animal interacts with the substrates in its environment (Bezanson 2017), the conditions of captivity and the common substrates present therein may have significant impacts on mobility and positional behaviors in arboreal primates (Vereecke et al. 2011). On a physiological level, the rigid substrates characteristic of captivity appear to alter the skeletal morphology of chimpanzees, including by reducing the size of the palmar radoiocarpal ligament insertion sites, and increasing the sizes of the articular surfaces of the distal ulna and tibial plateau (Casado et al. 2021; Lewton et al. 2017). Mobility, activity, and exercise are notably related to physiological health in both humans and chimpanzees (Ely et al. 2013). As mentioned previously, captive chimpanzees have notably high occurrences of cardiovascular disease, compared to their wild counterparts (Strong et al. 2020). Encouraging mobility and locomotion, along with other approaches to alleviating stress, could be important means of addressing these health issues (Neal Webb and Schapiro 2023). Mobility, or the ability to engage in physical activities and locomotor behaviors if one chooses, signifies a chimpanzee's proper functioning of skeletal musculature and connective tissues (Hopper et al. 2022). Chimpanzees especially experience reductions to mobility as they reach old age (Magden et al. 2013). Impairments to mobility, therefore present a target for improving physiological health in chimpanzees, particularly for geriatric, injured, pathology-inflicted, and obese individuals.

Treatments that effectively treat mobility impairments in humans, like acupuncture therapy, have shown similar effects in chimpanzees (Magden et al. 2013). Neal-Webb et al. (2020) showed the promise of incorporating physical activities into positive reinforcement training to enact physical therapies for chimpanzees. Chimpanzees with mobility issues demonstrated increased mobility and ease of movement after undergoing the physical therapy program. Behavioral indicators also signified more positive welfare states after the chimpanzees received physical therapy. It is possible that such mobility-focused therapies could improve health outcomes and even help to prevent strain and future mobility impairments prophylactically, just as physical therapy does in humans (Jamtvedt 2008; Vogel et al. 2009). As Hopper et al. (2022) confirmed in their assessment of the residents at Chimp Haven, evaluating movement fluency and mobility through caregiver ratings could be used to effectively monitor health and welfare. Additional efforts can then be made to address these identified mobility issues. In humans, moderate to high intensity exercises that address but do not exacerbate injuries are recommended by physical therapists to improve mobility (de Vries et al. 2012). Mobility aids and structural accommodations may be used to encourage independent movement and overall wellbeing when one suffers from a mobility impairment (Boerema et al. 2017; Satariano 2012). The built environment can be an important impediment or facilitator of independent movement, physical activity, and sustained mobility in elderly humans (Brownson et al. 2009). It is likely that incorporating more usable structural aspects into a chimpanzee's environment would have a similarly positive therapeutic impact on their mood and mobility (de Vries et al. 2012; Neal Webb et al. 2018).

For chimpanzees, the more orthograde and arboreal behaviors that constitute a great deal of the variety of their physical activities in the wild are dependent on the prevalence of appropriate arboreal substrates (Saunders et al. 2017). The interplay between mental welfare, the structural composition of enclosures, and mobility is sufficiently apparent to warrant increased efforts toward improving mobility and welfare via the installation of therapeutic structural enrichment. If the easily climbable and preferred aspects of arboreal environments can be mimicked in sufficient abundance in captivity, these may effectively encourage improved and sustained mobility in chimpanzees while also incurring other linked welfare benefits.

2.1.8.3 Centrality of Environmental Interactions

This study is concerned primarily with the use of spatial and positional characteristics of enclosures and their inhabitants to promote welfare. These are of prime importance because of the drastic difference in environment between captive and natural contexts, as well as the intersection between spatial characteristics, positional expressions, and other welfare approaches and metrics.

The previously outlined sources of distress that are not necessarily caused by the environmental setup in the proximate sense may still be impacted by the environment and animals' spatial positioning within it. Physiological health metrics are impacted by physical activity and one's ability to move within their environment. Without sufficient space to move and substrate configurations to exercise movements on, an individual will face deteriorating physical conditions associated with poorer cardiovascular health and general mobility (Neal Webb and Schapiro 2023; Reamer et al. 2022). If a species has evolved to use a specific set of positional behaviors in particular ecosystems, the expression of natural species-typical behaviors requires an environment that is conducive to these same behaviors. Such an environment is necessary for satisfying physical needs and the mental desire to perform species-typical physical actions. It is also necessary to emphasize mobility in captive animals as a means of facilitating agency. An animal that can easily move through their environment and alter their spatial position at will can exercise more impactful freedom of choice for what and with whom they choose to perceive and interact. This choice may be explored by researchers to effectively design more usable spaces to encourage other aspects of chimpanzee welfare.

Complex enclosure structures that facilitate arboreal-like behaviors may offer enrichment value in their visual and tactile presence as well as through the unique positional interactions that chimpanzees may have in relation to the structures. Given that cognitive abilities in apes have been hypothesized to have been partially motivated by the complex information processing that occurs when navigating arboreal environments in the manner that apes do (Potts 2004), providing complex three-dimensional spaces to navigate could act as an important enrichment tool. By encouraging movement throughout an enclosure at will, climbable structures also allow for different perceptive experiences from different vantage points.

In socially housed primates, spatial and structural configurations can also have an impact on interactions between individuals (Beisner et al. 2023; Caws et al. 2008; Neal Webb et al. 2018). Best practices for designing enclosure spaces highlight the need for including multiple paths of travel, particularly so animals have potential escape routes when they are involved in agonistic events (AZA Ape Tag 2010). Sufficient space is necessary for individuals to separate enough to avoid conflict and increased occurrence of abnormal behaviors that result from social tension (Caws et al. 2008; Duncan et al. 2013; Neal Webb et al. 2018). Conflicts may be avoided if antagonists have the option to reduce the amount of time they spend sharing experiences with one another. Reductions in violent conflicts and sufficient mobility to escape from aggressors can also lower the chances of individuals sustaining detrimental injuries from fights. An environment that discourages agonistic conflict would likely be less stressful to live in and would help to maintain the physical health of individuals. Furthermore, for primates in zoos, the presence of view obstructing features can provide animals the ability to alter their positions to control the public’s view of them, thereby lowering the negative impacts of the visitor effect on zoo animals

(Cairo-Evans 2022). In all such cases, the ability for captive animals to achieve the benefits of the structural aspects of an enclosure, requires the actualization of their capabilities at performing positional behaviors to effectively move about their environment.

The priorities of different approaches to captive animal welfare intersect with the spatial configurations and compositions of the enclosures in which the animals reside. Efforts to encourage greater physical health, produce desired ranges of stress-related hormones, discourage stress-related behavior, increase frequencies of positive behavioral indicators of welfare, provide enriching experiences, allow chimpanzees to make impactful decisions, and promote the expression of species-typical behaviors may all be enhanced when individuals occupy appropriate enclosures that support the actualization of the benefits of the most common approaches to improving welfare. Similarly, when designing and constructing spaces for captive primates like chimpanzees, one should consider the interconnectedness of environmental characteristics with the sources of negative and positive welfare that one experiences while occupying the enclosure in order to maximize the potential positive impact of implementing features into the environment.

2.1.8.4 Impediments to Prioritization

While sufficient environmental conditions and usable space are recognized to be important factors in animal welfare, it is difficult to assess the myriad ways the designs of enclosures can impact primate welfare. However, efforts to do so are necessary to put appropriate environmental changes into practice.

Studies seeking to determine the impact of changes to major enclosure conditions often analyze animal behavior before and after enclosure change (e.g. Earl et al. 2020; Jensvold 2001;

Neal Webb 2018; Ross et al. 2010; Videan and Fritz 2007). This approach is valuable for showing the impact of the overall environment on individual welfare, but reliance on expensive whole-enclosure renovations or construction limit the applicability of these studies to institutions that are able and willing to enact expensive changes. When the impacts of enclosure changes and upgrades are investigated, it is difficult to determine the effects of particular characteristics of the enclosures because of their coincidence with other enclosure characteristics. If an institution intends to implement smaller-scale changes, they may have difficulty in effectively directing their efforts. Moreover, the traditions of captivity often result in feasible comparisons largely between different captive individuals to determine if captive conditions are adequate. As such, acceptable conditions and welfare scores are largely restricted to subjects living among the commonly available environmental features already present in captivity.

For large and destructive apes especially, the robust structural enrichment necessary for its safe provisioning to the enclosed group often requires substantial material and installation costs. Moreover, the effectiveness of enrichment can most easily be judged by frequent observations of its use (Kemp 2023). The nature of cheaper non-structural enrichment, particularly feeding devices, may be more conducive to occupying an ape’s time and attention because of their greater manipulability and goal-directed use (Kemp 2023). Temporary non-structural enrichment is also easier to incorporate into a captive environment and can have more immediate and easily observable effects on behavior, especially in the form of feeding devices, compared to structural additions (Celli et al. 2003).

Enclosure upgrades that are undertaken may still result in residents failing to utilize all of their available space and structures (Duncan et al. 2022; Ross et al. 2011). Individuals who have spent sustained periods of their lives in enclosures with limited space and structural features may refrain from using the full extent of their enclosures (Duncan et al. 2022). Despite the difficulty of focusing efforts toward spatial and structural sources of welfare, these may be of critical importance to producing humane living conditions, particularly when synthesized with other welfare focuses. While behavioral changes in more spacious and complex enclosures may be more subtle than one might hope, such efforts may be important for satisfying certain prerequisites to optimum environments. Once these prerequisite conditions are met, other efforts at expanding one's use of their environment may be better targets for improving welfare (Duncan et al. 2022). If more targeted and quantifiable metrics were used for assessing positional behavior and enclosure element qualities, a potentially critical avenue for improving welfare could be more thoroughly explored.

2.2 Study Focuses

This thesis seeks to advance the understanding of the relationship between environments, positional behaviors, and welfare in chimpanzees. I aimed to gather information that would be beneficial for promoting the welfare of the study subjects and chimpanzees under human control broadly. In pursuit of this goal, I examined the impact of installing a new climbing aid into a chimpanzee enclosure at Chimp Haven, the design of which was informed by known tendencies in chimpanzee environmental interactions and locomotor mechanics. In addition, I analyzed the relationships between individual chimpanzee subjects, their engagement with available substrates, and positional behavior. These data were used to create individual profiles for positional behaviors and substrate use to better tailor caretaking efforts to the needs of individual chimpanzees. Positional behavior profiles were also generated for each observed substrate used by the subjects. Finally, I developed a metric for analyzing the expression of positional behaviors and substrate use to infer welfare based on measures of behavioral diversity.

2.2.1 Using Wild Positional Behaviors to Inform Climbing Aid Design

The pursuit of a complex captive environment that encourages species-typical positional behaviors may be best aided by considering known tendencies in their expressions among wild conspecifics. Captive enclosures tend to be limited both by cost and human cultural tendencies for constructing and using environments more broadly (Brando and Coe 2022). This may partially explain the prevalence in enclosures of rigid, uniform structures with angular, particularly orthogonal, intersections (Vereecke et al. 2011). While this phenomenon is not universal, established construction materials and practices favor it as the outcome when constructing enclosures (Brando and Coe 2022).

Humans' culturally bound and common preferences for characteristics of the environments that they occupy may not be entirely disparate from those of chimpanzees. Both wild and captive chimpanzees also spend large portions of their time in terrestrial contexts (Hunt 1992; Kosheleff and Anderson 2009; Meulman et al. 2012). Captive adult chimpanzees tend to show a preference for more stable, rigid substrates that have little chance to change form in ways that are difficult to predict (Ross and Lukas 2006). These tendencies may reflect the safety advantage of terrestriality, wherein individuals are less likely to lose balance, fall, or sustain injuries from falls when on the ground (Anderson 2018). Arboreal locomotion is not only more dangerous but can require greater energy expenditure while facilitating relatively lower travel distances (Pontzer and Wrangham 2004). However, when occupying trees, chimpanzees are at low risk of predation (Pruetz et al. 2008; Stewart and Pruetz 2013). They can also gain access to high-value foods that are best foraged from fruiting trees (Green et al. 2020; Newton-Fisher 1999). The energetic costs associated with extensive and intensive locomotion of both arboreal and terrestrial types are investments that can result in net fitness advantages (Janson 2007).

Chimpanzee anatomy reflects their adaptations for both terrestrial and arboreal forms of locomotion (Holowka et al. 2017). Arboreal adaptations, like high intermembral indices, long and curved phalanges II-V, rigid lower backs, and highly abducted halluces enhance the safety and biomechanical efficiency of arboreal locomotion (Friesen et al. 2022; Hunt 1991).

Some types of arboreal locomotion are more costly than others. Descending a tree likely carries relatively little energetic cost, as these locomotor modes can be driven primarily by gravity and momentum (Neufuss et al. 2017; Preuschoft 2002). This is particularly the case for suspensory-capable swinging apes like chimpanzees (Hunt 1992). Traveling at a constant height within an arboreal setting can carry only a moderate energetic cost depending on the structural makeup of the tree branches used (Hanna and Schmitt 2011). This may be more efficient than terrestrial travel, as quadrupedal locomotion on large-diameter horizontal substrates appears to be less strenuous than terrestrial quadrupedal locomotion in bonobos (Schoonaert et al. 2016). This is likely because the grasping abilities of the panin foot allow greater traction on rounded substrates compared to flat ones (Schoonaert et al. 2016).

The most energetically costly forms of arboreal locomotion in large primates like chimpanzees involve overcoming the force of gravity on one's body (Hanna and Schmitt 2011). The least cost preferred routes to greater elevations have been reported to occur through quadrupedal ascension on inclined (<45°) branches and trunks (Hunt 1992). Alternatively, apes may ascend in a primarily vertical direction along trunks or branches (Neufuss et al. 2018).

When available, apes will manually grasp onto secure, near horizontal branches and branching points on a tree that allow them to apply propulsive forces through their limbs with minimal risk of losing balance as their body swivels about the wrist (Hunt 1992; personal observation). This "ladder" style vertical climbing is primarily driven by the hindlimbs while the hands operate within a smaller range of motion likely employed for balance and to pull one's body in line for the next pedal step (Hunt 1992). Depending on branch compliance, using easily grasped thin horizontal supports in this manner likely provides security and minimizes the energetic cost of balance-correcting movements. When climbing vertically along the trunk of a tree, apes tend to take advantage of secure handholds in the form of knots and branches along the vertical route (personal observation).

A bare trunk can present more of a challenge to climb, but primate morphologies have evolved to meet this challenge (Hanna et al. 2017). When climbing a vertical trunk, apes hold onto the back or side of a trunk with their hands and feet. To propel themselves upward, they push against the trunk with their hindlimbs and pull against it with their forelimbs (Hanna et al. 2017). Individuals are able to sustain their position on the trunk from the frictional contact between their volar skin and the vertical substrate (Cartmill 1979). This friction is generated partly by the grasping force applied to the trunk by the hands and feet (Holowka et al. 2017; Neufuss et al. 2017). Additional frictional forces are created based on the ape's distribution of weight throughout their body (Cartmill 1979). The grasping foot allows for weight to be applied in a direction that promotes more friction between the foot and the substrate while also allowing for the translation of propulsive forces into more vertical directions (Holowka 2017). While the hindlimbs tend to push the body's center of mass away from the vertical substrate during ascension, the forelimbs pull the body up and towards the trunk (Neufuss et al. 2017). When an ape suspends their body away from the hand that is in contact with the substrate in a direction that deviates from vertical, they can generate greater frictional forces between the two surfaces (Cartmill 1974; Newton's second law). The hand can act as an anchor that counters propulsive forces that push away from the substrate as well as maintain balance while free limbs move through the portions of their gait that do not involve contact with the substrate (Granatosky et al. 2018). However, this requires the hand to maintain sufficient contact with the substrate. With increasing weight pulled against the hand, more grip strength is required to maintain its grasp (Cartmill 1979). Applying weight away from the substrate about the hand allows for the manual frictional contact necessary for the body to press and pull on the trunk to generate greater lift (Cartmill 1974). A balance must be maintained so that the applied pressure used to generate enough frictional force to ascend the tree does not rely on insufficient hand strength and overwhelming loading demands (Cartmill 1979). This system involves the energetically expensive application of strength in opposing directions in order to sustain a body's attachment to a vertical substrate. These demands, along with the energetic demands of moving a large body vertically against the gravitational forces acting upon it, sum to a costly but feasible locomotion strategy for primates (Hanna and Schmitt 2011).

The severity of this issue depends on the diameter of the vertical substrate being climbed. Apes tend to prefer climbing on thinner diameter substrates, provided they can support their weight (Hunt 1992; Thorpe and Crompton 2006). For small diameter supports, an ape's hand may be able to grasp around a large enough portion of the circumference in a manner that provides greater ability to apply pressure to the substrate and create an anchor with the substrate with lower effort (Hunt 1991; Hunt 1992; Isler 2005). In this case, more weight does not need to pull away from the hand to create adequate frictional forces, particularly because sufficient frictional force can be generated from applying enough adduction force over a great enough portion of the circumference of the substrate (Cartmill 1979). As such, smaller diameter supports tend to involve a more flexed elbow arm configuration when climbing (Isler 2005). Large diameter supports are less preferentially climbed and more difficult to ascend because one's grips are not as secure to the trunk (Hunt 1992). Therefore, one must push their body further away from the trunk, usually through employing an extended elbow type climbing, to generate enough friction between their hands and the substrate to allow them to climb (Cartmill 1974; Cartmill 1979; Hunt 1991). Consequently, on larger diameter vertical substrates more energy must be expended to both push away from the trunk and maintain a strong enough hand grip to bear this weight's application in a direction that actualizes the minimum frictional force necessary for climbing. This likely explains apes' preference for climbing the less energetically demanding thin vertical supports (Hunt 1992; Thorpe and Crompton 2006). However, large diameter logs are often used when constructing climbing structures for captive chimpanzees due to the strength and durability that make their provisioning to the apes safe (Brando and Coe 2022). Altering enclosure structures based on known preferences in wild chimpanzees may aid in creating more safe and usable climbing apparatuses that encourage vertical climbing behaviors.

2.2.2 Positional Behavior and Substrate Use Profiles

The notable impacts of mobility and physiological health on the apparent quality of life of both humans and chimpanzees warrants further investigations into the welfare implications of the ways that chimpanzees utilize their bodies. Assessments of mobility and movement fluency are valuable and cost-effective ways to identify changes to the state of an individual’s positional behaviors (Hopper et al. 2022; Neal Webb et al. 2020). However, these do not provide an assessment of the characteristics of the specific positional behaviors in which one engages, but rather their combined effect. The outward expression of positional motifs both demonstrates and sustains one’s ability to perform these actions (Mayer et al. 2011). If one fails to use their bodies in particular ways, they may lose an effective aspect of their mobility that allows them to exercise control over their own body and its position in the environment. This would result in a loss of freedom to make impactful choices that is hypothesized to lead to negative emotional states (Neal Webb et al. 2020).

The ape body is a complex of movable parts that are both differentiated and interconnected in a way that results in a mobile whole (Myatt et al. 2012). This is why one can assess the summative mobility of a chimpanzee (Hopper et al. 2022). However, to maintain functioning as a whole, the functioning of individual parts must also be in order. Redundancy allows for an individual to maintain overall spatial abilities despite the loss of certain aspects of their mobility (Ang et al. 2017). However, simultaneous loss of mobility throughout the body, as can happen in old age, may have more detrimental effects, especially when combined with further mobility impairments from sustained injuries (Neal Webb et al. 2019).

While more subjective mobility scoring systems may also be effective for assessing the use of more targeted areas of the body, determining the conditions of these body elements would require one to observe and assess larger positional behaviors that involve using the body part in a specified way. For example, one can note a chimpanzee’s failure to bear weight on a particular foot while standing. However, other mobility impairments may have more subtle impacts on expressed positional behaviors. If utilizing a part of the body in a certain way causes discomfort, an individual may refrain from entering postures and locomotor forms that involve this manner of body element use. This would result in the masking of mobility impairments despite their presence. As an example, a chimpanzee could incur an injury while engaging in suspensory behavior such that hanging from their hand causes them pain. If this individual avoids suspensory behavior on that particular limb, caretakers could fail to catch this mobility impairment as the chimpanzee would not demonstrate the behavior. Instead, one would see a chimpanzee engaging in normal compressive use of that limb and note no issues with its use.

I hypothesize that collecting data on the types of limb engagement and axial body use in chimpanzees can be used to create positional behavior profiles for individuals. With this information, captive management programs could identify changes to positional tendencies, including as a result of injuries and senescence. On top of the utility of recording frequencies of positional behaviors on their own, these frequencies may also be used to calculate the diversity of positional behaviors. Thereby, quantitative evaluations of positional behaviors can allow for simpler comparisons between individuals. The method outlined in this study focuses more on the characteristics present in expressed postures rather than locomotion tendencies. While it may be useful to understand locomotor characteristics, such a task is difficult to perform in detail by eye in real time (Vereecke et al. 2011). Comparing gaits requires quality video footage of individuals moving in a standardized direction (Vereecke et al. 2011). Such a scenario is rare enough to make this strategy unfeasible. Further, this would only be used to capture particular gaits and movement types on the target substrate. An incomplete profile of an individual's locomotor behavior necessarily emerges. Given the link between certain postural features and physical exertion abilities in humans (e.g. Sidlauskiene et al. 2019), physical issues that alter an individual's ability to bear weight on parts of their bodies in particular ways may result in observable patterns in the expression of both postures and locomotion. Given this relationship, I propose that the body's engagement in different postures could reflect other positional and mobility-related qualities of individual chimpanzees because of the common factors that restrict both mobility in locomotion and one's ability to engage in specified postures. The fact that chimpanzees both in more wild and more captive environments spend the majority of their time in stationary postures (Neal Webb and Schapiro 2023) also highlights the feasibility and potential benefits for collecting data on postural engagements over locomotor forms. In addition to relative ease of collection, focusing more heavily on chimpanzees' stationary postures allows a larger amount of data to be collected and interpreted compared to what can be noted about moving subjects without high resolution video footage (Cheyne 2011).

While many metrics for determining physiological health in captive apes require invasive actions or the acquisition of difficult to procure samples, observational data on body part use could be used to monitor recovery from mobility impairing injuries in a less intrusive manner. Even in the absence of acute mobility impairments, under-use of a body's natural capabilities can result in degenerating mobility (Mayer et al. 2011). Benefits may arise for welfare-focused management programs if they could identify positional behaviors that are underutilized by an individual, whether due to present impairments or not, in order to encourage their more frequent long-term use. The means of achieving this may include the aforementioned strategies of physical therapy focused positive reinforcement training, acupuncture therapy, structural modifications to an enclosure, and motivated use of such structural modifications (Brando and Coe 2022; Jensvold et al. 2001; Kemp 2023; Magden et al. 2013; Neal Webb et al. 2020).

Common problems for animal rehabilitation include neophobia, novel stimuli aversion, and substrate avoidance. Avoidance of particular areas and substrates by some apes is an issue that many caretakers are familiar with. An animal that was brought up under certain environmental conditions may be averse to utilizing the available variety of stimuli and substrates (Duncan et al. 2022). Duncan et al. (2022) contend that restricted space use is not caused by anxiety towards particular substrates but rather a spatial learned helplessness, wherein individuals act under the constraints put on them by stressors from past environments. However, reliance on the familiar is often a part of an avoidant response characteristic of anxiety disorders and the long-term cyclical persistence of stimulus-related anxiety and avoidant behaviors (Krypotos and Engelhard 2018; Scheveneels et al. 2016). Anxiety related to unfamiliar substrates is a particularly noticeable issue for rehabilitating dogs rescued from breeding mills (Wormald et al. 2016). These canines will often fear the unfamiliar, opting to maintain contact with concrete grounds when possible. Such cases commonly require intensive training and drug intervention to get the dogs comfortable with occupying and urinating on naturalistic surfaces.

A chimpanzee’s willingness to engage with unfamiliar stimuli has previously been used to characterize their personality (Hopper et al. 2014; Massen et al. 2013). Traits constituting personality are attributed to not only an individual’s innate disposition, but can also depend on their age, sex, and estrous state (Hopper et al. 2014). Given that traits regarding interactions with environmental features change over medium to long-term periods of time, it is apparent that these tendencies are not fixed or completely innate. This is further evidenced by the fact that chimpanzees have tendencies to use their environments in ways that may be limited depending on the conditions under which they were raised (Duncan et al. 2022; Morimura and Mori 2010). Differing tendencies to engage with novel or varied stimuli may impact the effectiveness of provisioned enrichment, as the enrichment can only benefit the welfare of a chimpanzee if they are willing to engage with it. Therefore, the ability to monitor changes to a captive chimpanzee's tendencies to engage with more novel aspects of their environment would be beneficial for evaluating and promoting this aspect of their overall welfare, and would inform the presumed likelihood that a given individual will incur benefits from provisioned enrichment.

The use frequencies of structural additions to enclosures may underwhelm caretakers if the structure is not appropriate or the animals choose to avoid it due to unfamiliarity (Duncan et al. 2022). Apes may develop patterns of substrate preference and enclosure use that carry on even as enclosures change (Duncan et al. 2022; Ross et al. 2011). While it is necessary to try implementing new types of structural enrichment to enclosures, their sheer cost can transform the additions into high-stakes ventures. It is therefore sensible for captive management programs to invest resources in other types of enrichment with more predictable and apparent positive impacts on the animals. However, if one could better predict the effects and use of structural elements, one could design and implement better structural additions with greater benefits to the animals. Such insights may be achieved by recording frequency profiles and diversity scores for an individual chimpanzee's substrate and enclosure space use.

An animal's expressed positional behaviors are the intermediaries between the internal motivations of an animal and their interactions with their environment (Bezanson 2017). Therefore, the spatial and structural features of an environment will impact the positional behaviors that an animal can and tends to use. With greater emphasis placed on this link, positional behavior expressions may be used to assess the structural makeup of an enclosure. While it is sensible that the structural composition within an environment impacts an animal's positional behavior, mobility, and welfare, the literature is lacking in detailed comparisons of positional repertoires depending on the environment's characteristics. Despite this, it may be necessary to more fully understand the ways that enclosure features may be used by chimpanzees in order to design spaces conducive to the expressions of species-typical positional behaviors, greater physical health, and more positive mental states.

2.3 *Concluding Remarks*

Much like humans, chimpanzees are long-lived animals with complex internal emotional states that are affected by sustained impacts from past experiences (Spiezo et al. 2021). The impacts of specific features of their environments and individual chimpanzees' interactions with these features have notable but not fully explored effects on the physiological and psychological welfare of chimpanzees. Given the amount of control that captive management programs have over the lives of their resident chimpanzees, caretakers are obligated to maximize efforts to improve individual chimpanzees' experienced wellbeing. The extractive nature of captivity, particularly for former biomedical laboratory specimens, magnifies the human obligation to provide optimum conditions for the remainder of these subjects' lives. As these individuals are reaching geriatric ages, it is urgent to employ known effective strategies for promoting welfare, as well as explore new metrics and enrichment types, such as those presented in this study, in pursuit of a more complete, holistic approach to welfare improvement efforts.

Chapter 3: Methodology

3.1 Study Site: Chimp Haven

Data were collected at Chimp Haven, a nonprofit sanctuary that houses chimpanzees formerly used for biomedical research in the United States (ChimpHaven.org, n.d.). This research was funded largely by the National Institutes of Health (NIH) for the study of infectious diseases like the human immunodeficiency virus (HIV) and hepatitis B and hepatitis C (Turner 2023). Chimp Haven is located within Caddo Parish in Keithville, Louisiana in the northwestern portion of the state. At a latitude of 32°20' N, the sanctuary is located within a humid subtropical climate, characterized by hot and humid summers and mild but variable winters (Beck et al. 2018). During the present study, the average daily maximum temperature was 36.4º C (heat index of ~ 41.1º C), and the average daily minimum temperature was 25º C, with an average dew point of 21.9º C (Wunderground.com, n.d.). Chimp Haven is located in the Eddie D. Jones Nature Park, which contains forest composed of primarily of loblolly pine, oak, elm, sweetgum and maple trees (Horvath et al. 2007).

At the time of this study, Chimp Haven housed approximately 320 chimpanzees, making it the largest captive sanctuary housing chimpanzees globally (ChimpHaven.org, n.d.). Most residents at the facility are the retired subjects of biomedical research, particularly HIV/AIDS research, the federal funding for which was phased out in 2015 (NIH.gov, n.d.). A small number of chimpanzee residents at Chimp Haven were involved in cognitive research, and even fewer were formerly kept as pets. Most details on the specific nature of the research and living conditions of chimpanzees while in the care of the various research laboratories are unknown due to these details being subject to redaction based on the laboratories' discretion.

Table 3.2.1 Subject Sex and Age

Subject	Sex	Age (yr)
Apache	Male	39
Cliff	Male	41
Coco	Male	31
Dino	Male	30
Fancy	Female	30
Gary	Male	30
Jake	Male	32
Jane	Female	36
Maggie	Female	39
Marsha	Female	37
Novella	Female	28
Peewee	Male	42
Pumpkin	Female	33
Shone	Male	30
Simpson	Male	30
Zort	Male	39

Chimp Haven is a non-breeding facility. As such, its female residents take oral birth control medication, and its male residents are vasectomized. Pregnancies have occurred only four times at the facility due to failed vasectomies. Long lifespans, lack of reproduction, and generally late age at first arrival mean that much of the population are geriatric. While some of the older chimpanzees were brought into captivity after being captured in the wild when they were young, most residents at Chimp Haven were born in captivity.

3.2 Study Subjects

The group observed in this study consisted of 16 chimpanzees as presented in Table 3.2.1. The members of this mixed-sex group were reared in single-sex groups until their eventual arrival and merging at Chimp Haven (Chimp Haven staff, personal communication).

3.3 Study Enclosure

This study was conducted in the enclosure designated as the C200 corral, where chimpanzees also have access to indoor rooms in the C2 annex. The outdoor area has an open top, measures approximately 0.3 acres, and contains two climbing structures and a central canopy. The lowest portion of the walls around the perimeter are comprised of rigid metal mesh with interspaced portions of flexible metal mesh (FlexMesh). Feeding troughs are welded to parts of the rigid metal mesh. Metal shelves are affixed to the interior of the perimeter walls at multiple points. Additional enrichment, especially interactive feeding devices (fishers), are periodically attached to the outer side of the metal mesh. The large upper portions of the perimeter walls are made of flat wood panels and metal sheets such that chimpanzees cannot climb out of the enclosure. The portion of the perimeter wall that is shared with the indoor area is composed of solid concrete blocks. About 3 feet of concrete ground extends from the perimeter of the outdoor enclosure along approximately half of the perimeter's total length closest to the indoor enclosure areas.

Climbable platform structures are located near the northern and southern ends of the enclosure (Figure 3.3.1 A-D). They contain four platform levels, with two rectangular platforms on the first level, two on the second level, one on the third level, and three on the fourth level. A long ramp extends from ground level to the platform on the first level. A second, shorter ramp connects a platform on the second level to the platform on the third level. Platforms are held up by 11 wooden telephone pole-like posts. Horizontal metal bars extend from select portions of the wooden posts. A hammock is hung on level two of each platform structure. Each of the two platform structures are mirror images of the other. A tall canopy is positioned in the center of the

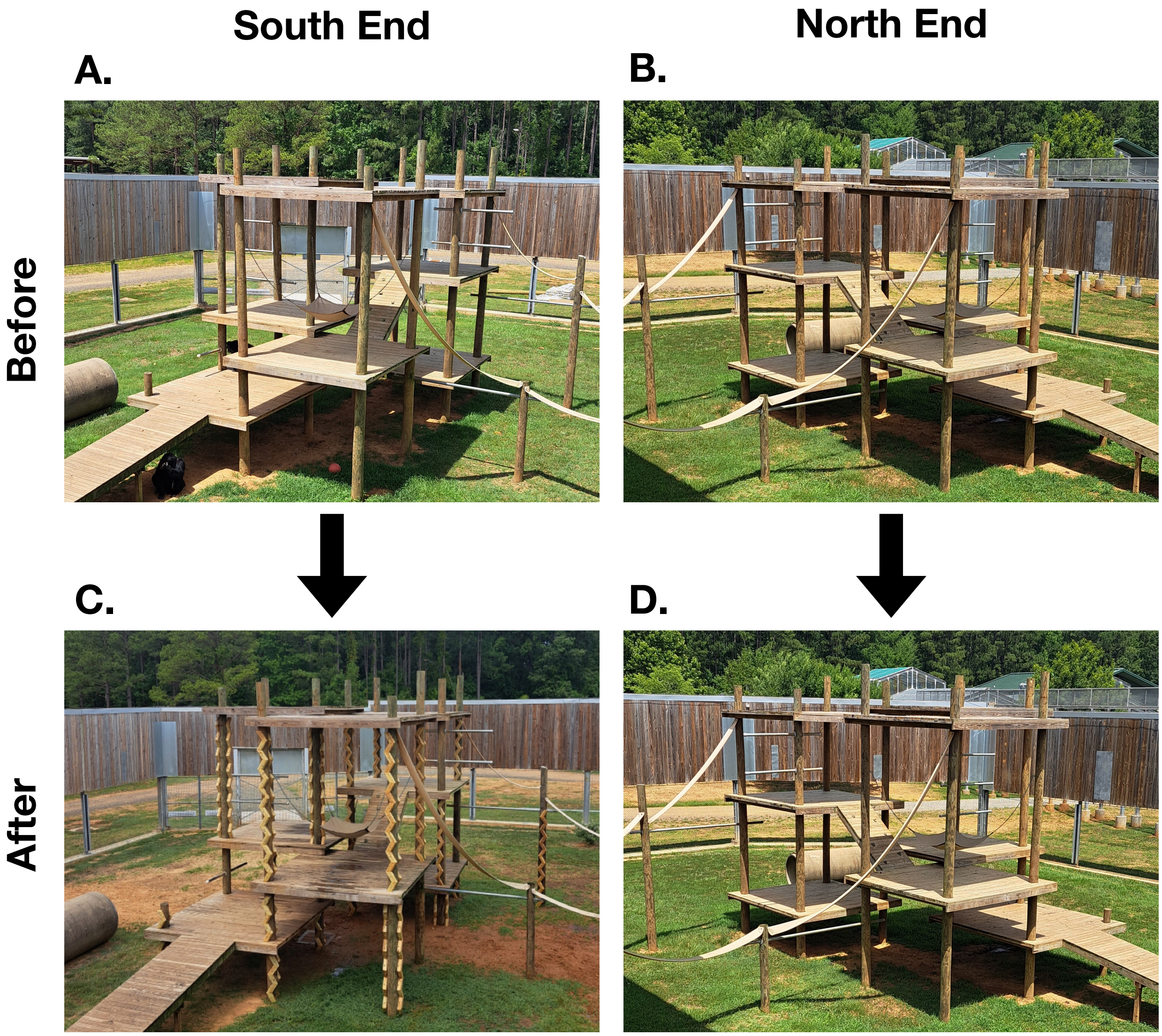


Figure 3.3.1 **A.** The south platform structure before the installation of the climbing aids. **B.** The north platform structure before the installation of the climbing aids onto the south platform structure. **C.** The south platform structure after the installation of the climbing aids. **D.** The unchanged north platform structure after the installation of the climbing aids onto the south platform structure.

outdoor enclosure between the two platform structures. A hammock hangs from the metal posts of the canopy close to ground level.

There are five indoor bedrooms that the chimpanzees have access to. The floors of the bedrooms are concrete and partially covered with daily-replenished straw bedding. The wall facing the indoor hallway is made of metal mesh with attached feeding troughs. The walls between bedrooms are comprised of perforated metal sheets. The remaining walls are concrete. Different bedrooms are outfitted with metal shelves, hammocks, and fire hose to allow for chimpanzees to climb and rest at different elevations indoors. There are multiple waterspouts that the chimpanzees can operate located indoors and along the exterior-facing concrete wall between the indoor and outdoor enclosure areas. Chimpanzees have constant access to all indoor and outdoor areas except during times that cleaning and maintenance activities are performed in the bedrooms or outdoor area.

3.4 Climbing Aid Design

I targeted ascent by vertical climbing as the locomotor form to be facilitated by the climbing aid. Vertical ascent is more comparatively energetically expensive than descent and constant height arboreal locomotion (Pontzner and Wrangham 2004). If treated as the limiting factor to arboreal locomotor behaviors, promoting vertical ascent would presumably also permit greater expression of descending locomotion. Furthermore, this would create more effective usable space and its associated potential social benefits (Caws et al. 2008).

The novel climbing aid was intended to facilitate easier and safer vertical climbing on a substrate more appealing than the bare medium-large diameter wooden columns that hold up the platform structures in the enclosure. Consistent with chimpanzees' preference for climbing thin supports (Hunt 1992), I chose to construct the novel climbing aid out of relatively thin (8-12 cm diameter) wooden garden posts. Attaching these to the sides of the large wooden columns was

$$F=\mu N \tag{1}$$

$$N=mg \tag{2}$$

$$N=mg\cos\theta \tag{3}$$

$$F=\mu mg\cos\theta \tag{4}$$

F = Frictional force of the volar skin with the substrate
N = Normal force acting on the body by the substrate
m = Mass of the body
g = Acceleration due to gravity

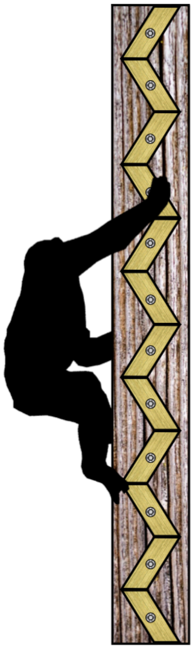


Figure 3.4.1 A profile view of the of the vertical climbing aid's design and its intended use.

meant to make their ascension and descension more favorable for the study subjects. Rather than running the garden posts parallel to the larger wooden column, segments of the posts were oriented in a zig-zag pattern (see Figure 3.4.1). This was chosen to amplify some of the beneficial aspects of thinner diameter supports. As a handhold deviates from a strictly vertical orientation, less effort needs to be put towards generating the sufficient normal force necessary to create enough friction between the substrate and the hand to resist the pull of gravity on the mass of the climbing body (Cartmill 1979; see equations 1-4 below).

Static friction between a completely horizontal handhold and a connecting grip is relatively easy to maintain because the force of gravity is applied in an overall more antiparallel direction to the resultant normal force acting on the hand by the substrate surface (Cartmill 1974). However, exclusive use of such handholds was not thought to be conducive to an overall vertical climbing gait form that is more typical of forest-dwelling chimpanzees. Wild chimpanzees will use branching points in trees that have these characteristics while engaging the vertical climbing gait. These grip points offer security when weight is pulled beneath them, but enable less vertical range of motion under heavier loads. In order for such horizontal grips to be efficiently climbed through their exclusive use, they must be positioned close enough together, much like a ladder. In an arboreal context, the use of horizontal handholds by great apes is more often integrated with the use of other substrate orientations. Horizontal handholds can be used exclusively along the branches of trees, but these will be present in a number of positions relative to the body. In the case of trees with many horizontal grip points clustered on the trunk, these could be safely used, but the gait's high turnover frequency associated with placing one's hands and feet only on these horizontal grip points may be more energy intensive than utilizing longer gaits that incorporate other gripped substrate orientations. Therefore, angled handholds were used to make generating frictional forces easier for the chimpanzees while also enabling enough vertical range of motion in the wrist to encourage vertical climbing up the pole.

At the same time, a partially restricted vertical range of motion was thought to encourage continued movement up the climbing aid. When one's center of mass is relatively more elevated with respect to one's hand position, the weight born on a highly abducted wrist makes for a less effective and controlled support of the body. Therefore, an individual climbing on the zig-zag structure would be compelled to raise their arm again to a more comfortable and effective position above the body, thus perpetuating the gait until they reach the next highest platform. If an individual must stop along the height of the wooden column and climbing aid complex, they can still grasp partly onto the joints between segments, or the tops or undersides of the segments angled vertically away from the body. In this way, halted movements up the climbing aid would

Figure 3.5.1 Climbing aid segments were pre-fabricated before installation

be expected to result in a combined forelimb suspension and cling posture commonly employed by captive and wild chimpanzees (Sarringhaus et al. 2014).

3.5 Climbing Aid Materials, Construction, and Installation

The climbing aids were prefabricated over two weeks outside of the enclosure prior to installation (see Figure 3.5.1). The lengths of the climbing aids were determined by measuring the heights of each pillar section on a platform structure in a separate enclosure that mirrored the intended structure modified for this study. The wood portion of the climbing aid consisted of non-uniform pressure treated garden posts that were relatively inexpensive compared to other commercially available supportive wood options. The garden posts were oblong, with cross-sectional lengths of 3.5 inches and cross-sectional widths of 2.5 inches. The sides along the width of the posts were mostly flat while the sides along the length were rounded.The garden posts were cut on 60° angles to create segmented units that were ~8.5 inches long each.

The joints between any two connecting units were fastened by two 1/4 inch by 6-inch zinc plated lag screws. Countersinks were drilled into the garden post units at the sites of lag screw insertion. These sites were off-center to minimize the chances of the two opposing lag screws colliding when fastened. Zinc plated washers of 1 inch diameter sat flush against the countersink. The lag screws were inserted on angles slightly deviating from the long axis of the wooden units such that they penetrated the near center of the mass of wood that could be reached by the length of the lag screw from the insertion site. Units were joined to create climbing aid segments of the necessary length to fit the wooden pillar sections between platform levels on the target climbing structure. Joints were sanded to prevent injury to the chimpanzees during use.

The climbing aids were installed during the 10-day period when the study group was held in a separate enclosure. This move was previously scheduled to allow for an unrelated construction project to take place, wherein a more effective drainage system was installed into the outdoor corral. I, along with several members of the behavior and maintenance teams at Chimp Haven, installed the prefabricated climbing aids onto the available bare column portions of the platform structures in the corral (see Figure 3.3.1 C.). The north end platform structure was left unmodified and acted as a control for this study (see Figure 3.3.1 D.). Climbing aids were not installed on the pillar sections that already contained metal bars affixed at some point along the span of their height. Each climbing aid segment was affixed to the wooden columns by an additional 1/4 inch by 6-inch zinc plated lag screw in the center of every garden post unit. The installers pulled on the climbing aids to ensure a minimum ability to sustain a portion of the strength of destructive chimpanzees. Notably, the climbing aids proved durable during data collection and the months following their installation.

3.6 Data Collection: Column and Platform Structure Use

In order to address Hypothesis 1, the novel climbing aid's efficacy was estimated by noting the frequency at which the subjects occupied different elevation levels on the platform structure, as well as the frequency at which they ascended and descended between the levels. Data were also collected on the nature of platform level changes (ascend, descend, climb using horizontal metal bar, climb using only wooden supports, use of ramps, jump, and drop). Additionally, platform level changes were categorized according to whether or not they occurred as a part of a chase/fight event. The number of individuals occupying each of the four platform levels was determined using 10-minute instantaneous scan samples. Platform level changes were recorded via continuous sampling over 30-minute periods.

Data were collected by reviewing video recordings of the focal areas from the four security cameras that monitor the C200 corral. The cameras in the southeast and southwest corners of the enclosure provided a complete view of the southern platform structure to which the climbing aid was affixed. The northeast and northwest cameras provided a complete view of the control platform structure on the north end of the corral. The cameras provided adequate quality of footage to collect data on platform level occupation and changes, but video resolution was not of a high enough quality to identify all 16 individuals in the group. I reviewed 11 days of video footage before (June 27th to July 9th) and 14 days of video footage after (July 22nd to August 4th) the climbing aid's installation. Sampled footage covered the 5.5-hour time frame between 6:30 AM and 12:00 PM on any given day.

3.7 Data Collection: Positional Behavior and Substrate Use

Hypotheses 2-4 were addressed by collecting positional behavior and substrate use data using ZooMonitor, the data collection application developed by the Lincoln Park Zoo

(ZooMonitor.org). I carried out instantaneous scan sampling on focal subjects at 1-minute intervals during 20-minute focal sessions. At each scan, I noted the type of locomotion or posture with which the subject engaged, all substrates with which the subject was in contact, the zone of the enclosure the subject occupied, and the degree to which the subject was exposed to direct sunlight, shade, or partial shade. With two exceptions, all subjects were followed for 8 total focal sessions. Due to technological errors that occurred when saving data, recovering data, and compensating for lost data, only 7 focal sessions followed Jane, and 9 focal sessions followed

Table 3.7.1 Locomotor Mode Descriptions

Mode	Description
Aerial Leap	Subject is engaged in an airborne leap, where their body does bear significant weight on any substrate as they transfer from one stratum to another. L12
Bipedal	Subject is moving while primarily engaging their hindlimbs to bear their weight and perpetuate their gait. L3
Pronograde Walk	Subject's torso is in a pronograde orientation as they engage a regular, repeating gait that incorporates all four limbs, usually in a diagonal sequence. L1a
Pronograde Tripedal Walk	Subject's torso is in a pronograde orientation as they engage a repeating gait using two hindlimbs and one forelimb. L2a
Pronograde Scramble-Walk	Subject's torso is in a pronograde orientation as they engage an irregular gait, usually over an uneven substrate or combination of substrates. L1c
Pronograde Run	Subject's torso is in a pronograde orientation as they move at higher than normal speeds with a gait that includes an aerial phase. L5
Torso-Orthograde Suspensory	Subject moves about at a near constant elevation with their weight supported via suspension or clinging. Their torso is generally held in an orthograde position. L9
Vertical Climb Ascent	Subject ascends a substrate or series of substrates, usually with their torso in an orthograde orientations. L8a-f
Vertical Climb Descent	Subject descends a substrate or series of substrates, usually with their torso in an orthograde orientations. L8g-l

Descriptions end with their characteristic alphanumeric code(s) assigned in Hunt (1996).
Only observed locomotor modes are displayed.

PeeWee. All focal animal data were collected between sunrise and 11:30 AM to avoid the risk of the observer experiencing heat-stroke, dehydration, or other temperature dependent illnesses. Focal sessions were carried out between June 29th and July 8th before the climbing aid's installation and between July 22nd and August 4th after the group was returned to their original enclosure.

Elements of the positional behavior categories recorded were modified from Hunt (1996), with consideration to their use and modification by Thorpe and Crompton (2006) and Sarringhaus et al. (2014). When the focal subject was not stationary, its locomotion type was recorded among the categories present in Table 3.7.1. When stationary, the posture category was selected among those available in Table 3.7.2. Ischial engagement was noted during sitting postures, which included sitting on one's ischia, sitting with one's ischia on one's heels (squat), and sitting with their left or right ischium on the ipsilateral heel (side squat). Involvement of

Table 3.7.2 Postural Mode Descriptions

Type	Description
Arboreal	Subject is stationary while bearing most of their weight via suspension or clinging. The torso is generally in an orthograde or intermediate orientation. P8,P9,P10,P12
Lie	Subject is lying in a primarily pronograde posture with the majority of the weight of their torso resting against at least one supporting substrate. P13
Sit*	Subject is sitting with their torso in a mostly orthograde orientation. Weight is borne on their ischia or dorsal thigh. P1,P2
Orthograde Stand	Subject is standing with a vertically oriented torso. Their weight is primarily held above a horizontal support. P5
Pronograde Stand	Subject is standing with their torso elevated above the ground in a pronograde orientation. P4a

Descriptions end with their characteristic alphanumeric code(s) assigned in Hunt (1996).

*The "Sit" mode includes sitting directly on one's ischia as well as sitting with their ischia resting on their heels (squatting).

Table 3.7.3 Forelimb Engagement Ethogram and Descriptions

Type	Description
None	The arm is not in contact with any substrate.
Contact	The arm is in contact with the substrate without bearing significant weight.
Arm-Out	The elbow is extended and contact between the arm and the substrate is made along a significant portion of the length of the arm.
Compression	The arm supports the body's weight in a compressive manor with the elbow partially or fully extended.
Crouch	The arm supports the body's weight in a compressive manor with the elbow highly flexed and positioned dorsally relative to the glenohumeral joint.
Elbow/Forearm	The elbow is flexed and weight is borne on the elbow or forearm.
Cling	The elbow is in a flexed position and the hand grasps a support at a position inferior to of just above the glenohumeral joint.
Suspend	A significant amount of the body's weight is borne through suspension away from the point of the hand's grasp on a substrate. This usually occurs with the arm above shoulder height and the elbow mostly extended.
Clasp	The hand actively grasps onto another part of one's own body
Carry Object	The hand is engaged only in grasping and supporting the full weight of an object
Object Manipulation	The hand is engaged in manipulating an object in the subject's environment

Definitions are provided for each category of forelimb engagement.

one's torso and head were also recorded as any observed combination of leaning on one's back, leaning on one's ventrum, leaning on one's left side, leaning on one's right side, and leaning on one's head.

In all stationary postures, engagement of the subject's left and right arms and legs were recorded as the categories presented in Table 3.7.3 and Table 3.7.4, respectively. The ethograms used for recording limb engagements were chosen based on the common positional motifs used to delineate postural modes in Hunt 1996, Sarringhaus et al. 2014, and Thorpe and Crompton 2006. These included the conventions of compression, suspension, and clinging in all limbs.

Table 3.7.4 Hindlimb Engagement Ethogram and Descriptions

Type	Description
None	The leg was not held in contact with any substrate
Contact-Leg Out	With an extended knee, the leg is held in contact with the substrate without bearing a significantly larger portion of the individual's body weight than in present in that limb.
Contact-Leg In	With a flexed knee, the leg is held in contact with the substrate without bearing a significantly larger portion of the individual's body weight than in present in that limb.
Compression	Weight is borne on the leg in a compressive manner with the knee flexed to a minimal degree
Mid-Compression	Weight is borne on the leg in a compressive manner with the knee flexed to a moderate degree
Bent-Compression	Weight is borne on the leg in a compressive manner with the knee flexed to a high degree
Knee	The knee is flexed and weight is borne on the knee or anterior tibia
Cling	The hindlimb is flexed and grasps onto the substrate
Suspend	A significant amount of the body's weight is borne through suspension away from the point of the foot's grasp on a substrate.
Clasp	The foot actively grasps onto another part of one's own body
Carry Object	The foot is engaged only in grasping and supporting the full weight of an object
Object Manipulation	The foot is engaged in manipulating an object in the subject's environment

Definitions are provided for each category of hindlimb engagement.

Compressive modes of the forelimbs were subdivided into a standard compression and a crouched position. Leg compression was separated into the modes of compression, mid-compression, and bent-compression based on the degree to which the knee was bent. Hunt's (1996) use of the leg engagement categories of "in" and "out" were abandoned in favor of recording the different types of compressive hindlimb use. "In" and "out" were defined in this thesis as non-weight bearing engagements of the hindlimb with different degrees of bending at the knee (see Tables 3.7.3 and 3.7.4).

Table 3.7.5 Available Substrates and Their Descriptions

Code	Substrate Type	Description
WdCA	Climbing Aid	Novel zig-zag shaped climbing aids.
WdCS	Wood Column (Side)	Sides of the rounded wooden columns.
WdCT	Wood Column (Top)	Circular tops of the rounded wooden columns.
WdP	Wood Platform	Flat surfaces composed of wooden planks fastened to orthogonal wooden beams underneath
WdR	Wood Ramp	Inclined flat surfaces composed of wooden planks
CCI	Concrete Culvert (In)	Interior rounded surface of a concrete culvert.
CCO	Concrete Culvert (On)	Exterior rounded surface of a concrete culvert.
CG	Concrete Ground	Flat ground made of concrete
CW	Concrete Wall	Flat walls made of concrete
MB	Metal Bar	Flat or rounded bar made of metal
MCh	Metal Chain	Hanging chain made of metal
MCo	Metal Column	Vertical column made of metal
MFM	Metal FlexMesh	Fence-like flexible metal mesh woven from thin wires to give the material elastic properties
MM	Metal Mesh	Durable fence-like metal mesh assembled in a square grid pattern and oriented vertically
MSh	Metal Shelf	Horizontal flat shelf made of a metal frame and inset metal mesh
Di	Dirt	Dirt Ground
Gr	Grass	Ground mostly covered in grass
Hm	Hammock	Durable hanging canvas
FH	Fire Hose	Thick hanging fire hose
PlDv	Plastic Divider	Thick square plastic divider used by care staff to close or open doorways
WS	Water Spout	Spout by which water is provisioned through Chimpanzee operation
Fd	Food	Material meant to be eaten
OCh	Other Chimp	Cohabitant Conspecific
OO	Other Object	Manipulable object in the environment
DU	Data Unavailable	Viewer was unable to note the substrate used

The first column includes the unique code used to designate a given substrate

During each scan, I recorded all substrates with which the subject's body was in contact (for the list of all substrates considered, see Table 3.7.5). The zone of the enclosure in which a subject resided was also recorded in accordance with those highlighted in Figure 3.7.1 and Figure 3.7.2. Finally, sunlight exposure during a given scan was recorded as: in sunlight, in shade, or in partial shade.

3.8 Data Categorization

Testing Hypotheses 2-4 required the designation of descriptive stationary posture categories based on the combination of posture type, axial body engagement, and limb engagement. Multiple classification schemas were generated depending on what constituent elements were considered and which of these were pooled versus split when designating posture categories.

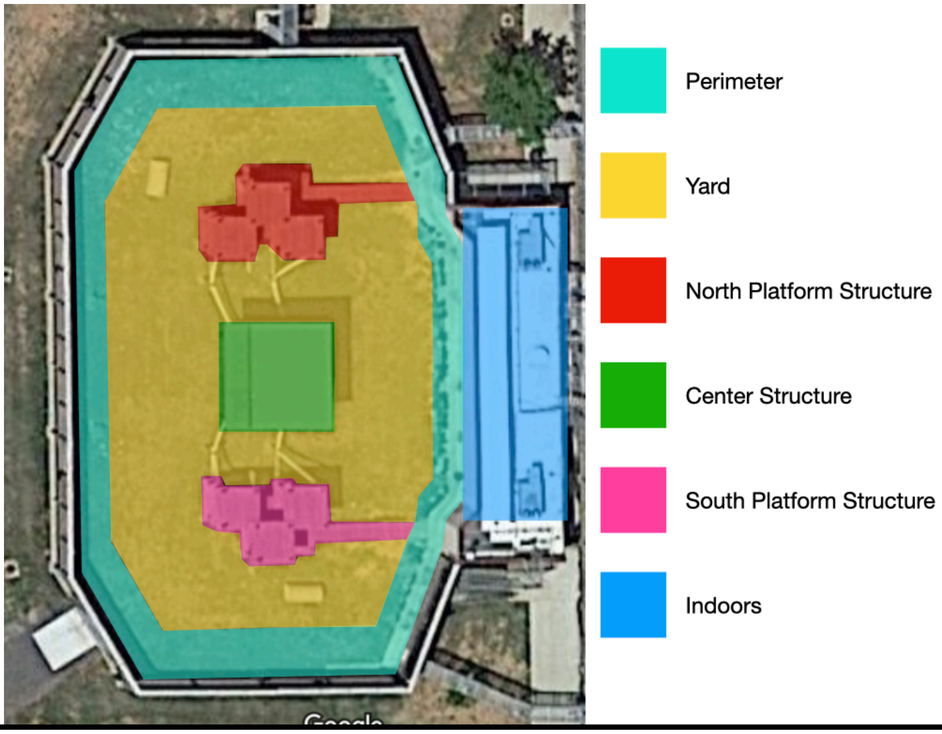


Figure 3.7.1 The designated zone areas within the study enclosure. Colors correspond to the zones listed on the right.

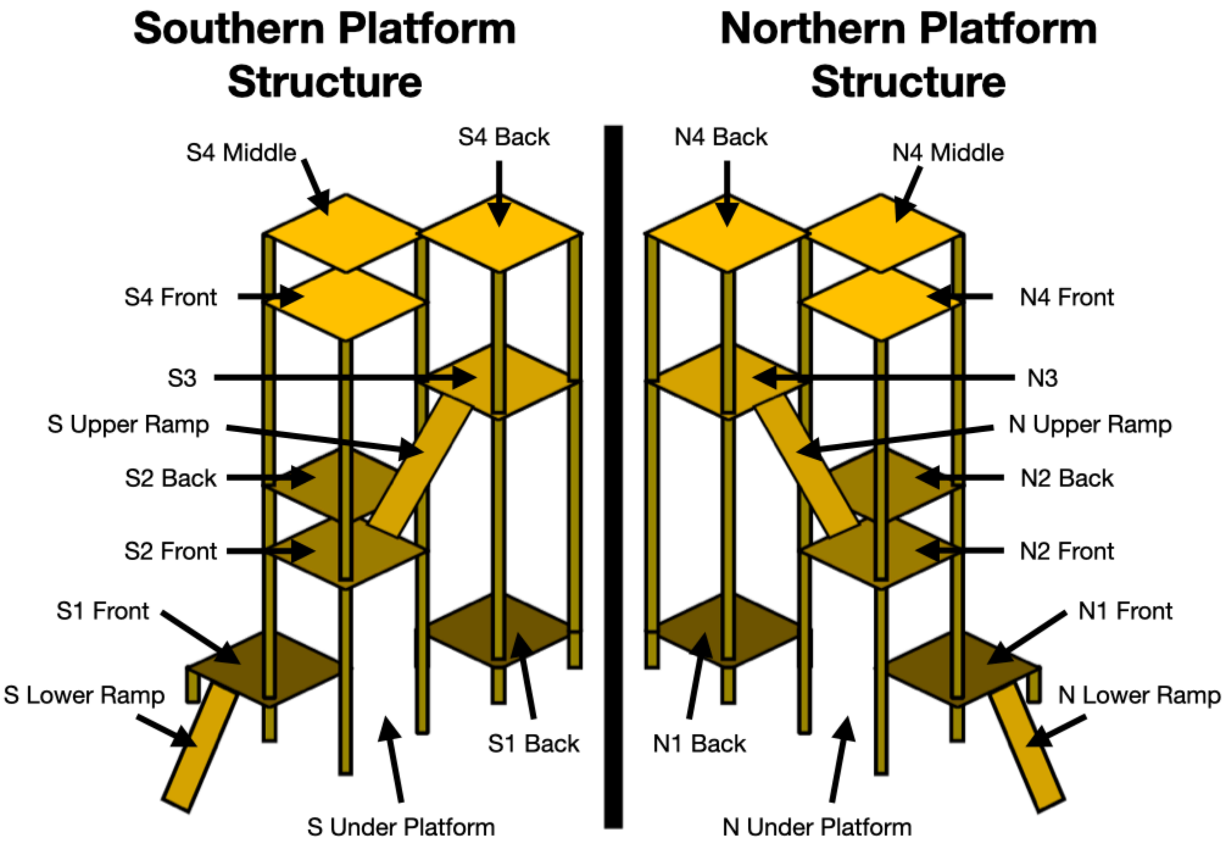


Figure 3.7.2 The designated zones within the platform structures at each end of the enclosure.

For this report, eight positional classification schemas (Pos1-8) were used to categorize observed positional behaviors (see Table 3.8.1). These varied based on the prioritization and inclusion of different positional motifs employed in stationary postures. Pos1 was the most expansive schema, which tended to incorporate the largest number of positional elements into its naming conventions. Pos2 excluded leaning and heel use types in its designations. Pos3 focused on the engagement of limbs in ways indicative of higher weight bearing. Arm contact and leg categories of "in" and "out" were not considered. Pos4 was based on the closest approximation of the recorded data in this study to the positional categories described in Hunt (1996). Pos5 emphasized hindlimb engagements to a greater degree than Pos1, while Pos6 emphasized

Table 3.8.1 Positional Mode and Positional Motif Classifications

Positional Classification Schema	Description
Pos1	Contains the most detailed positional categories that considers broad positional modes, major limb engagement types, and axial body engagements, with mirrored postures pooled. See List S3.8.1.
Pos2	Contains the same positional categories as Pos1, but excludes the impact of axial body leaning and sided squatting. See List S3.8.2
Pos3	Contains broad positional modes with the addition of major limb engagements not entirely typical of the positional mode. See List S3.8.3
Pos4	Contains the positional modes consistent with Hunt's (1996) standardized positional modes. See List S3.8.4
Pos5	Contains broad positional modes combined with detailed engagements of the hindlimbs. See List S3.8.5
Pos6	Contains broad positional modes combined with detailed engagements of forelimbs. See List S3.8.6
Pos7	Contains basic positional modes with the addition of torso and squat leaning. See List S3.8.7
Pos8	Contains the most basic positional modes. See List S3.8.8
Limb and Axial Body Engagement	**Description**
Right Forelimb	Engagement type for the right forelimb
Left Forelimb	Engagement type for the left forelimb
Right Hindlimb	Engagement type for the right hindlimb
Left Hindlimb	Engagement type for the left hindlimb
Axial Body Engagement	Combination of leaning types using portions of the axial body
Limb Combination	**Description**
Any Forelimb	Pooled engagement of a given forelimb
Any Hindlimb	Pooled engagement of a given hindlimb
Both Forelimbs	Simultaneous engagement of both forelimbs
Simultaneous Hindlimb Engagement	Simultaneous engagement of both hindlimbs
Ispilateral Limb Engagments	Simultaneous engagement of both hindlimbs
Contralateral Limb Engagements	Simultaneous engagement of both hindlimbs
All Limbs Combined	Pooled engagement of all four limbs

forelimb engagements to a greater degree. Pos7 included general positional categories, while Pos8 included only the basic recognized positional modes.

In addition to the eight complete positional classification schemas, positional behavior tendencies were also compared using individual limb engagements and their combinations. Limb use combinations included the pooled engagements of both forelimbs, the pooled engagements of both hindlimbs, the combined engagements of all limbs, the pooled ipsilateral limb engagements, and the pooled contralateral limb engagements. Substrate use data was organized by both the combination of substrates with which a subject engaged and the presence or absence of engagement with each particular substrate. Two enclosure zone categorization schemas were considered based on the pooling and splitting of the different platforms on the two structures.

3.9 Data Analysis

Student's T tests were used to determine if there was a significant difference between the rates of elevation level changes on the south (experimental) platform between the periods before and after the introduction of the climbing aid. These tests were also performed to compare the rates of elevation level changes on the north (control) platform throughout the study. Student's T tests were employed to compare the relative rates of elevation level changes between the north and south platform structures both before and after the introduction of the climbing aid.

In a similar manner, Student's T tests were used to compare the average rates of occupation for each platform structure and each level of the two platform structures between the periods before and after the introduction of the climbing aid. Comparisons were also made for relative rates of occupation between the north and south platform structures during the period before and during the period after the climbing aid was installed. Mean rates of platform level changes involving the use of metal bars or only wooden supports were compared via T tests under conditions that considered only ascents and only descents.

For each platform structure, the proportion of ascents and descents involving the use of metal bars or exclusively wooden supports were compared using T tests between the periods before and after the introduction of the climbing aid. This was done in order to infer any climbing aid-dependent changes to the means by which subjects tend to climb on the platforms. Additionally, the average number of elevation level changes involved in fights per trial and per elevation level change were compared using Student’s T tests between the periods before and after the climbing aid’s installation on each platform structure, and between the two platform structures during both periods of the study.

Chi square tests were performed to compare the relative rates of occupation for each platform level on the two platform structures. Comparisons of the rates of occupation were made between the observed values and the mean expected values, as well as the expected values corresponding to an even distribution over space between the four platform levels. These tests were used to determine the relative occupation rates of the platform structures overall as well as in the periods before and the climbing aid was installed.

Differences in the rates of the subjects’ occupation of enclosure zones and degrees of sunlight intensity were both determined by performing Chi-square analysis and comparing the generated Pearson residual values. These tests were also performed to compare differences in enclosure zone occupation and sunlight exposure for the collective of male chimpanzees and the collective of female chimpanzees as well as for the group as a whole between the periods before and after the installation of the climbing aid.

Chi-square tests were also performed to compare the rates of expression for individuals' positional behaviors under the different positional classification schemas. The relative rates of basic locomotion and posture engagement between individuals were also compared via Chi-square tests. Additional analysis of positional behavior elements was performed by comparing Pearson residual values from Chi-square tests for the frequency of occurrence of limb engagement types by each individual limb, the pooled engagement of any arm, the pooled engagement of any leg, the simultaneous engagement of both arms, the simultaneous engagement of both legs, the pooled simultaneous engagement of ipsilateral limbs, and the pooled simultaneous engagement of contralateral limbs. The final limb use comparison made involved the use of Chi-square and Pearson residuals to determine the degree to which each individual exhibited sidedness in their forelimb and hindlimb use. When relevant, Chi-square tests were performed to compare positional expressions between the collective male and collective female subjects. Additional Chi-square tests were performed as necessary to determine the difference in positional expression for the entire group between the periods before and after the introduction of the climbing aid.

Tendencies of substrate use and substrate combination use were compared between individuals using Chi-square tests and resultant Pearson residuals. The relative propensities for different substrates to coincide with the expression of different positional behaviors and limb use types were determined by comparing the Pearson residuals from Chi-square tests of independence between these substrate and positional variables.

In keeping with Hall et al. (2021) and Miller et al. (2020), diversities of positional behaviors were calculated under each of the eight positional classification schemas and all limb use combination schemas using the Shannon diversity index (H). Pielou's evenness (J) was also calculated to supplement each reported Shannon diversity index. Diversity was also calculated for each individual under the Pos1 classification schema when truncated by broader positional types. Diversity and evenness scores were similarly calculated for each individual's substrate type use and enclosure zone occupation. Positional diversity was calculated for each substrate to determine the degree to which a given substrate is associated with a variety of positional expressions. The diversity indices that were calculated for every individual under each of the positional classification schemas were compared via linear regression to determine the degree of agreement between positional diversity measures (Lyman 2008).

3.10 Declaration of Noninvasive Research Status

This project was approved by the board at Chimp Haven, the Sanctuary Chimpanzee Care Committee (SCCC) and the NIH, who determined the research to be neither harmful nor invasive. Observational data on focal animal behavior were collected in person from outside of the outdoor enclosure and in the hallways adjacent to the indoor enclosure rooms. There were secure barriers between myself and the chimpanzees at all times. I made no physical contact with the chimpanzees at Chimp Haven at any time during this study. Appropriate personal protective equipment was worn at all times near the study enclosure to prevent disease transmission. I was visible from within the enclosure, and the study subjects were often aware of my presence. The sight of observers collecting behavioral data is not novel to the chimpanzees at Chimp Haven and my presence in this study did not diverge greatly from the typical routines that the chimpanzees experience. During data collection, I was able to report to Chimp Haven's staff all observed incidents of fight events between chimpanzees and any resultant injuries. This allowed the behavior and medical teams to address any reported threats to the wellbeing of the chimpanzees in the study group. Chimpanzees were not harmed by my presence or the new structural elements introduced to the enclosure.

Chapter 4: Results

4.1 Hypothesis 1: Column and Platform Structure Use

4.1.1 Platform Level Changes

I predicted that the addition of the climbing aid would have the immediate impact of increasing the frequency of climbing on the platform structure and would increase the tendency of chimpanzees to occupy the modified platform structure. However, this hypothesis was not supported by the data collected on the frequency of platform level changes.

The frequencies of platform level changes on the north and south end platform structures were not biased toward one over the other to a significant degree overall (p = 0.222), before the installation (p = 0.0813), or after the installation (p = 0.573; see Table 4.1.1.1). The combined level change frequency on the two climbing platforms was overall greater before the installation of the climbing aid than it was after installation (p = 0.00407; see Table 4.1.1.2). Figure 4.1.1.1 shows the difference in elevation level change frequency before and after the climbing aid's installation on both platform structures. The south end platform structure, to which the climbing

Table 4.1.1.1 The Frequency of Elevation Level Changes Compared Between Both Platform Structures During all Study Periods.

	South (Experimental)	Δ	North (Control)	Significance
Before	3.950	=	6.587	p = 0.0813
After	1.506	=	3.201	p = 0.573
Overall	5.457	=	9.788	p = 0.222

Frequency of elevation level change were calculated as the average number of platform level changes per 30 min trial period.
p-values were determined by comparing means via Student's T tests.
Bold p-values represent statistical significance at the 95% confidence interval
Cell shading represents the relative difference in values at the 95% confidence interval. Gray shading signifies that no significant difference was found between the two values. When a significant difference is present, the larger value is shaded I red, while the smaller value is shaded in blue.

Table 4.1.1.2 Frequency of Elevation Level Change Compared Between Both Study Periods for Each Platform Structure.

	Before	**Δ**	**After**	**Significance**
South (Experimental)	3.950	>	1.506	**$p = 4.61 \times 10^{-6}$**
North (Control)	6.587	=	3.201	$p = 0.0856$
Overall	10.537	>	4.708	**$p = 0.00407$**

See Table 4.1.1.1 for description of elevation level change frequency
See Table 4.1.1.1 for description of Significance column and cell shading.

aids were affixed, saw a decrease in level changes after the group's return to the enclosure ($p = 4.61 \times 10^{-6}$). Differences in platform level changes on the north end platform structure were not significant when comparing the period before and after the climbing aid's installation ($p = 0.0856$).

Throughout the course of this study, ascending via use of the horizontal metal bars that are attached to some portions of the wooden columns occurred more frequently than ascents

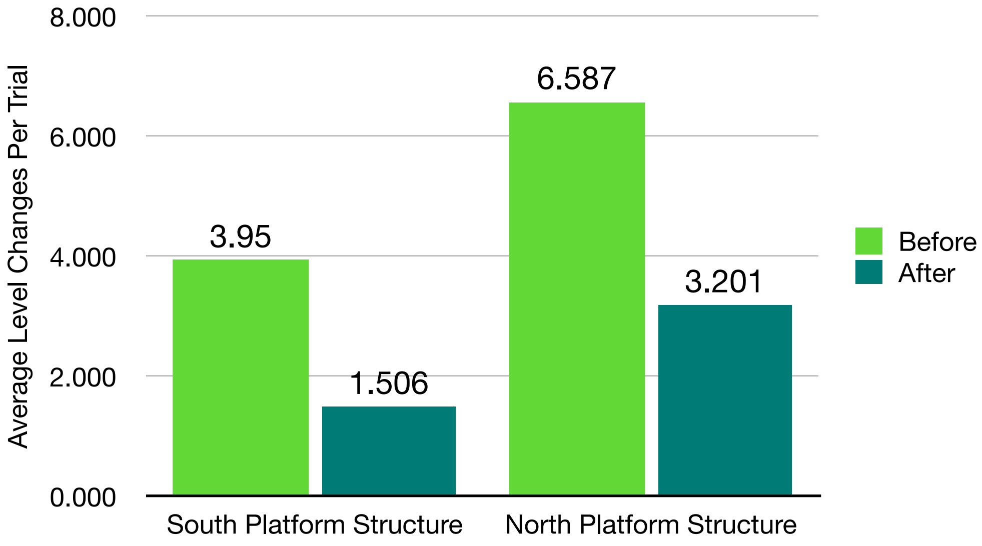


Figure 4.1.1.1 Frequency of elevation changes observed on both platform structures before and after the installation of the climbing aid.

Table 4.1.1.3 Difference in Climbing Means by Vertical Direction of Movement.

	Metal Bar	**Δ**	**Wood Supports**	**Significance**
Ascent	1.27273	>	0.70909	**$p = 9.13 \text{ x}10^{-4}$**
Descent	0.86182	<	1.23273	**$p = 0.0106$**

The combined rates of ascent and descent on all platform structures were calculated as as the average number of occurrences per 30 min trial period
See Table 4.1.1.1 for description of Significance column and cell shading.

involving the exclusive use of wooden supports ($p = 9.13 \text{ x}10^{-4}$; see Table 4.1.3). In contrast, descending was more likely to exclude the use of the metal bars, with the chimpanzees utilizing only wooden supports ($p = 0.0106$). Rates of level changes using only the metal bars were not considered, as use of the metal bars nearly always incorporated holding onto wooden supports as well.

The proportion of the total ascents observed that were associated with metal bar use remained unchanged after the climbing aid's installation for both the south end platform structure ($p = 0.675$) and the north end platform structure ($p = 0.774$; see Table S 4.1.1.1). The tendency to ascend using only wooden supports decreased on the south end platform structure ($p = 0.00234$), but the decrease in the proportion of ascents utilizing only wooden supports on the north end platform structure was not significant ($p = 0.0730$), after the group's return to the enclosure. The tendency to use only wooden supports when descending remained unchanged after the installation of the climbing aid for both the south and north platform structures ($p = 0.861$ and $p = 0.531$ respectively). Changes to the proportion of descents involving metal bar use was also insignificant for both the south and north end platform structures ($p = 0.134$ and $p = 0.433$ respectively).

Table 4.1.1.4 Total and Proportional Rates of Fight-Related Elevation Level Changes Compared Between Study Periods.

		Before	Δ	After	Significance
Total Fight Frequency	**Overall**	2.2231	>	0.2987	**p = 0.00407**
	South Platform Structure	1.0661	>	0.0584	**p = 0.00553**
	North Platform Structure	1.1570	>	0.2403	**p = 0.0313**
Proportional Fight Frequency	**Overall**	0.3375	>	0.0933	**p = 0.0140**
	South Platform Structure	0.2699	>	0.0388	**p = 0.0114**
	North Platform Structure	0.4389	=	0.1418	p = 0.0508

Total fight frequency was calculated as the average number of fight-related elevation level changes per 30 minute trial.
Proportional fight frequency was calculated as the average number of fight-related elevation level changes per total elevation level changes under a given condition.
See Table 4.1.1.1 for description of Significance column and cell shading.

After the group's reintroduction into their typical enclosure, the instances of platform level changes involved in fights decreased both in total numbers (p = 0.00407) and as a proportion of the total level changes (p = 0.0140; see Table 4.1.1.4). The total rate of elevation level changes involved in fights is represented in Figure 4.1.1.2. The trend of decreased fight-

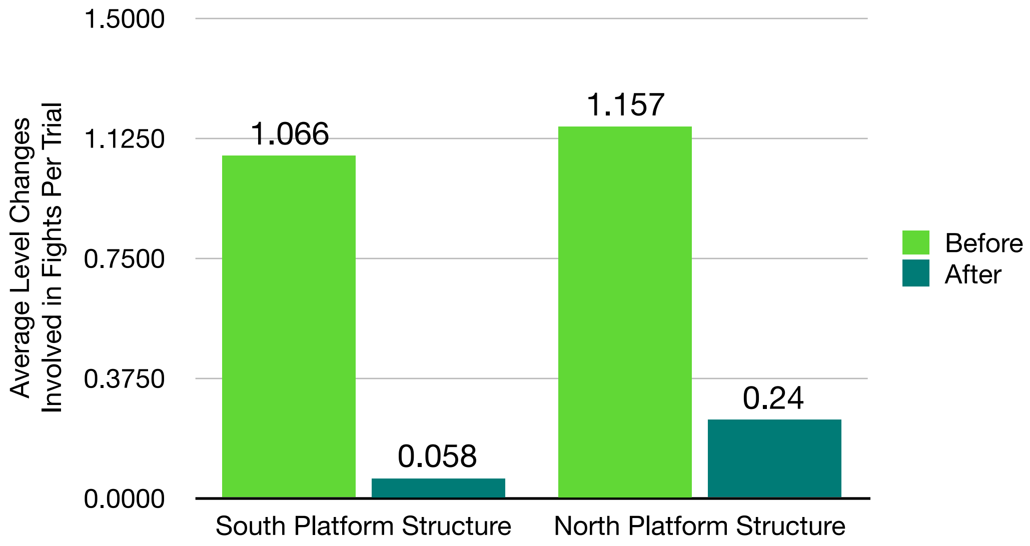


Figure 4.1.1.2 Rates of elevation changes involved in fights observed on both platforms before and after the installation of the climbing aid.

Table 4.1.1.5 Total and Proportional Rates of Fight-Related Elevation Level Changes Compared Between Platform Structures.

		South (Experimental)	Δ	North (Control)	Significance
Total Fight Frequency	**Before**	1.0661	=	1.1570	p = 0.879
	After	0.0584	=	0.2403	p = 0.247
	Total	0.5018	=	0.6436	p = 0.611
Proportional Fight Frequency	**Before**	0.2699	=	0.4389	p = 0.387
	After	0.0388	=	0.1418	p = 0.271
	Total	0.1944	=	0.3052	p = 0.212

See Table 4.1.1.4 for descriptions of the total and proportional fight frequencies.
See Table 4.1.1.1 for description of Significance column and cell shading.

related elevation level changes was characteristic of the south end platform structure (p = 0.00553), where fights accounted for a disproportionately larger amount of the total observed level changes before than after the group's reintroduction to their typical enclosure (p = 0.0114). After the installation of the climbing aid, fight-related level changes on the north end platform structure were less frequent (p = 0.0313), but the lower proportion of level changes involved in fights after the group's reintroduction did not cross the threshold of significance (p = 0.0508). Fight-related level change frequency was not significantly different between the north and south end platform structures throughout the study (p = 0.611; see Table 4.1.1.5), before the climbing aid's installation (p = 0.879), or after the climbing aid's installation (p = 0.247). The proportion of level changes involved in fights was not significantly different between the two platform structures overall (p = 0.212), before the climbing aid's installation (p = 0.387), and after the climbing aid's installation (p = 0.271).

4.1.2 Platform Level Occupation

The platform level occupation rates observed throughout this study also failed to support Hypothesis 1. Differences in elevation level occupation between the two platform structures during both periods of the study can be found in Table 4.1.2.1 and are represented in Figure 4.1.2.1. There was no significant difference between the chimpanzees' rates of occupying the north or south end platform structures overall throughout the entirety of the study (p = 0.158). The subjects occupied the south end platform structure more frequently than the north end platform structure before the climbing aid's installation (p = 0.000277). After the climbing aid was installed, rates of occupying the north end platform structure were higher compared to the south end platform structure, but this difference failed to reach the threshold of significance (p = 0.0528).

Table 4.1.2.1 Difference in Occupation Rates Between Platform Structures by Elevation Level.

Study Period	Elevation	South (Experimental)	Δ	North (Control)	Significance
Before	Level 1	0.5241	=	0.6043	p = 0.178
	Level 2	0.5401	>	0.1230	**$p = 6.34 \times 10^{-16}$**
	Level 3	0.1283	>	0.0775	**p = 0.0442**
	Level 4	0.0481	=	0.0481	p = 1.000
After	Level 1	0.3782	<	0.4475	**p = 0.0462**
	Level 2	0.2332	=	0.2899	p = 0.0545
	Level 3	0.0525	<	0.1134	**$p = 8.75 \times 10^{-13}$**
	Level 4	0.0441	>	0.0021	**$p = 6.29 \times 10^{-13}$**
Before	Total	1.2406	>	0.8529	**p = 0.000277**
After	Total	0.7080	=	0.8529	p = 0.0528
Entire	Total	1.9486	=	1.7058	p = 0.158

Occupation frequency was calculated as the average number of chimpanzees occupying the platform level(s) per 10 minute trial.
See Table 4.1.1.1 for description of Significance column and cell shading.

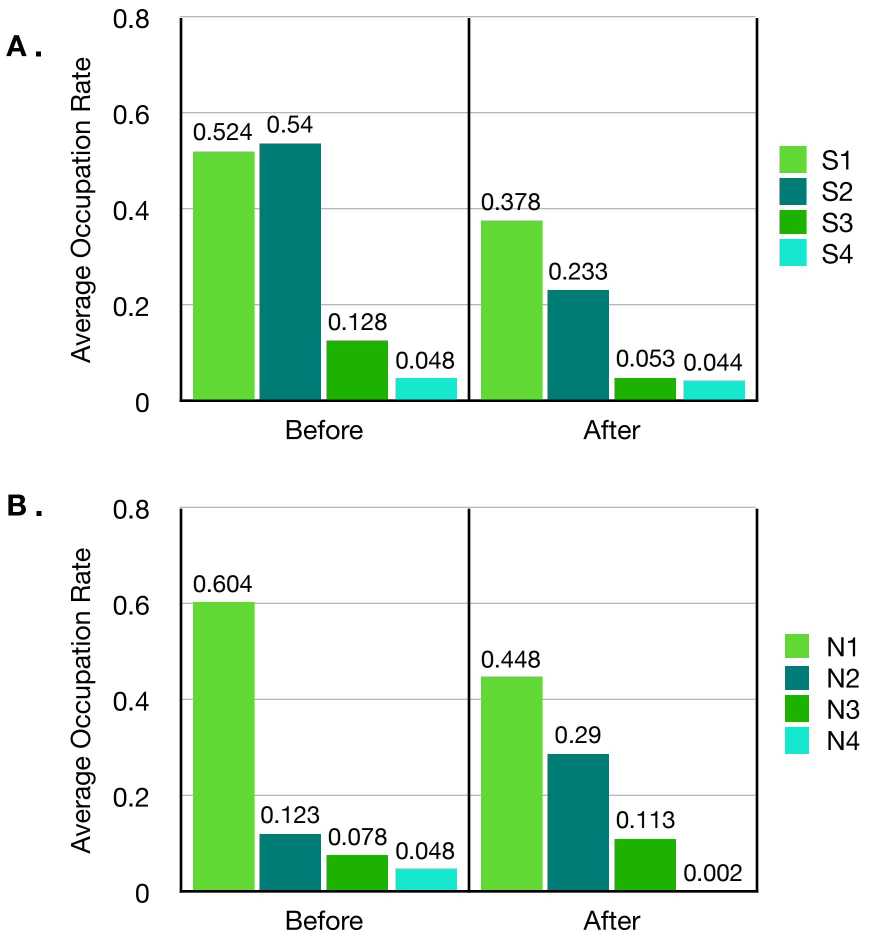


Figure 4.1.2.1 A. Rates of occupation for each elevation level before and after the installation of the climbing aid on the south end platform structure. **B.** Rates of occupation for each elevation level before and after the installation of the climbing aid on the north end platform structure.

The difference between occupation rates of the two platform structures at the same elevation levels are summarized in Table S4.1.2.1. Before the introduction of the climbing aid, data on preference for occupying the same elevation levels between platform structures revealed no tendency toward occupying level one on either the north or south end platform structures (p = 0.178). During this period, the second level of the south end platform structure was occupied more frequently than the second level of the north end platform structure (p = 6.34 x10^{-16}), and the same tendency to occupy the south end platform structure over the north end platform structure existed for the third elevation level ($p = 0.0442$). Occupation of the fourth elevation level was not significantly different between the two platform structures ($p = 1.000$).

After the climbing aid was installed, the chimpanzees tended to occupy the first level of the north end platform structure more often than the south end platform structure ($p = 0.0462$). The subjects did not show a significant preference for either platform structure when occupying the second elevation level ($p = 0.0545$). When on the third elevation level, the north end platform structure was occupied more frequently than the south end platform structure ($p = 8.75 \times 10^{-13}$). The chimpanzees occupying the fourth platform elevation level were seen more frequently on the south end platform structure ($p = 6.29 \times 10^{-13}$).

The combined rate of occupation for both platform structures was greater before than after the group was reintroduced into the enclosure ($p = 0.000311$; see Table 4.1.2.2). The rates at which the south end platform structure was occupied were greater before than after the climbing aid's installation ($p = 9.31 \times 10^{-8}$). The north platform structure showed no significant difference in its rates of occupation between the two periods of the study ($p = 1.000$).

The south end platform structure saw a reduction in rates of occupation after the climbing aid's installation for the first platform level ($p = 0.00508$), the second platform level ($p = 2.06 \times 10^{-10}$), and the third platform level ($p = 0.000577$). The difference between occupation rates on the fourth platform level of the south end platform structure were not significant between before and after the climbing aid's installation ($p = 0.802$).

On the north end platform structure, the first and fourth levels were occupied more frequently before than after the climbing aid's installation ($p = 0.00318$; $p = 5.99 \times 10^{-6}$). The second platform level on the north end structure was occupied more frequently after the climbing

Table 4.1.2.2 Occupation Rates for Each Platform Level Compared Between Study Periods.

Structure	Elevation	Before	Δ	After	Significance
South	**Level 1**	0.5241	>	0.3782	**p = 0.00508**
	Level 2	0.5401	>	0.2332	**p = 2.06 x10^{-10}**
	Level 3	0.1283	>	0.0525	**p = 0.000577**
	Level 4	0.0481	=	0.0441	p = 0.802
North	**Level 1**	0.6043	>	0.4475	**p = 0.00318**
	Level 2	0.1230	<	0.2899	**p = 2.57 x10^{-5}**
	Level 3	0.0775	=	0.1134	p = 0.104
	Level 4	0.0481	>	0.0021	**p = 5.99 x 10^{-6}**
South	**All Levels**	1.2406	>	0.7080	**p = 9.31 x10^{-8}**
North	**All Levels**	0.8529	=	0.8529	p = 1.000
Overall	**All Levels**	2.0936	>	1.5609	**p = 0.000311**

See Table 4.1.1.6 for description of occupation frequency
See Table 4.1.1.1 for description of Significance column and cell shading.

aid's introduction compared to before its installation (p = 2.57 x10^{-5}). No significant difference was observed between the occupation rates on the third platform level before or after the climbing aid was installed (p = 0.104).

In sum, reductions in occupation frequency for the combined platform structures were observed after the climbing aid was installed for the first platform level (p = 0.000176; see Table S4.1.2.1), the second platform level (p = 0.0397), and the fourth platform level (p = 0.0183). Only the third platform level did not change in occupation frequency after the introduction of the climbing aid (p = 0.1907).

The tendency for using any particular one of the eight platform levels did not follow an even distribution of preference ($p < 0.05$; see Table 4.1.2.3, Figure 4.1.2.1). Before the climbing aid's installment, occupation rates on the north end platform structure were highest on the first

Table 4.1.2.3 Divergence of Each Platform Level from an Even Distribution by Study Period.

	South Platform Structure				**North Platform Structure**			
	Level 1	**Level 2**	**Level 3**	**Level 4**	**Level 1**	**Level 2**	**Level 3**	**Level 4**
Before	9.918 (196)	10.525 (202)	-5.041 (48)	-8.074 (18)	12.951 (226)	-5.244 (46)	-6.962 (29)	-8.074 (18)
After	9.041 (180)	1.881 (111)	-7.043 (25)	-7.458 (21)	12.465 (213)	4.682 (138)	-4.034 (54)	-9.533 (1)

The occupation rates of different levels of the platform structures were significantly different from an even distribution of platform level occupation both before and after the introduction of the climbing aid (Chi-square test; $p < 0.05$).
Pearson residual values are displayed for each platform level before and after the climbing aid's installation.
Total counts of for occupying a particular platform level are provided in parentheses in each cell
More intense red shading corresponds to significantly greater relative frequencies of the behavior ($p < 0.05$), while more intense blue shading corresponds to significantly lower relative frequencies of the behavior ($p < 0.05$).

elevation level ($p < 0.05$). The second elevation level was more frequently occupied than the fourth elevation level ($p < 0.05$), and the occupation rate of the third elevation level was not significantly different from that of the second or fourth elevation levels ($p > 0.05$). The overall tendency for using the first elevation level of the north platform structure was greater than that expected under an assumption of equivalent occupation of all eight platform conditions ($p < 0.05$). The frequency of use for the other three elevation levels on the north end platform structure was less than expected under the same assumption ($p < 0.05$). After the group's reintroduction to their typical enclosure, each subsequent higher elevation level on the north end platform structure was occupied less frequently than the preceding elevation level ($p < 0.05$). During this period of the study, both the first and second elevation level were occupied more frequently than would be expected by chance ($p < 0.05$).

Before the climbing aid's installation, the first and second levels of the south end platform structure were occupied at higher rates than the higher elevation levels ($p < 0.05$), and were occupied more frequently than expected by chance ($p < 0.05$). The third elevation level was occupied more frequently than the fourth elevation level ($p < 0.05$), and both the third and fourth elevation levels were occupied less frequently than expected by chance ($p < 0.05$). After the climbing aid's installation, the first platform level was occupied at the highest rate ($p < 0.05$), which was more frequent than would be expected under the assumption of equivalent occupation of all platform conditions ($p < 0.05$). The second elevation level was occupied less often than the first level, but more often than the third and fourth level ($p < 0.05$). The frequency at which the second elevation level was occupied was not significantly different from that expected by chance ($p < 0.05$). The third and fourth elevation levels were occupied at comparable rates, but subjects were less commonly seen occupying these levels than expected by chance ($p < 0.05$).

The change in condition from before to after the installation of the climbing aid saw changes in the propensity for chimpanzees to occupy certain platform levels (see Table 4.1.2.4). I observed a decrease in the tendency for chimpanzees' occupation of the platform structures to include the second elevation level of the south end platform structure ($p < 0.05$) and the fourth level of the north end platform structure ($p < 0.05$). The probability of an individual's occupation of the platform structures to include the third and fourth elevation level was significantly higher after the introduction of the climbing aid ($p < 0.05$; $p < 0.05$).

Table 4.1.2.4 Difference in Platform Level Occupation Between Study Periods

	South Platform Structure				**North Platform Structure**			
	Level 1	**Level 2**	**Level 3**	**Level 4**	**Level 1**	**Level 2**	**Level 3**	**Level 4**
Before	0.221 (196)	3.267 (202)	1.723 (48)	-0.450 (18)	0.050 (226)	-4.982 (46)	-2.082 (29)	2.643 (18)
After	-0.227 (180)	-3.353 (111)	-1.768 (25)	0.462 (21)	-0.051 (213)	5.115 (138)	2.137 (54)	-2.713 (1)

The occupation rates of different levels of the platform structures during the period before and after the introduction of the climbing aid were significantly different from their combined average rates of occupation (Chi-square test; $p <<< 0.05$).
See Table 4.1.2.3 for description of cell contents and shading

4.2 Hypothesis 2: Positional Behavior Profiles

4.2.1 Positional Modes

Hypothesis 2 posited that individual chimpanzees would display significant differences in their positional behaviors. This hypothesis was supported by as subjects showed distinct profiles of positional behaviors under multiple classification types ($p < 0.05$). Figure 4.2.2.1 showcases the relative tendencies of individuals to engage in the most basic types of positional behaviors considered in this study ($p < 2.2 \times 10^{-16}$). Profiles of the expression of Pos8 categories differed between male and female subjects ($p < 2.2 \times 10^{-16}$; see Table 4.2.2.1) Males were far more likely than females to be found sitting, whereas females were much more likely to be found squatting ($p < 0.05$). Females were more likely to stand in a pronograde manner, occupy "arboreal"

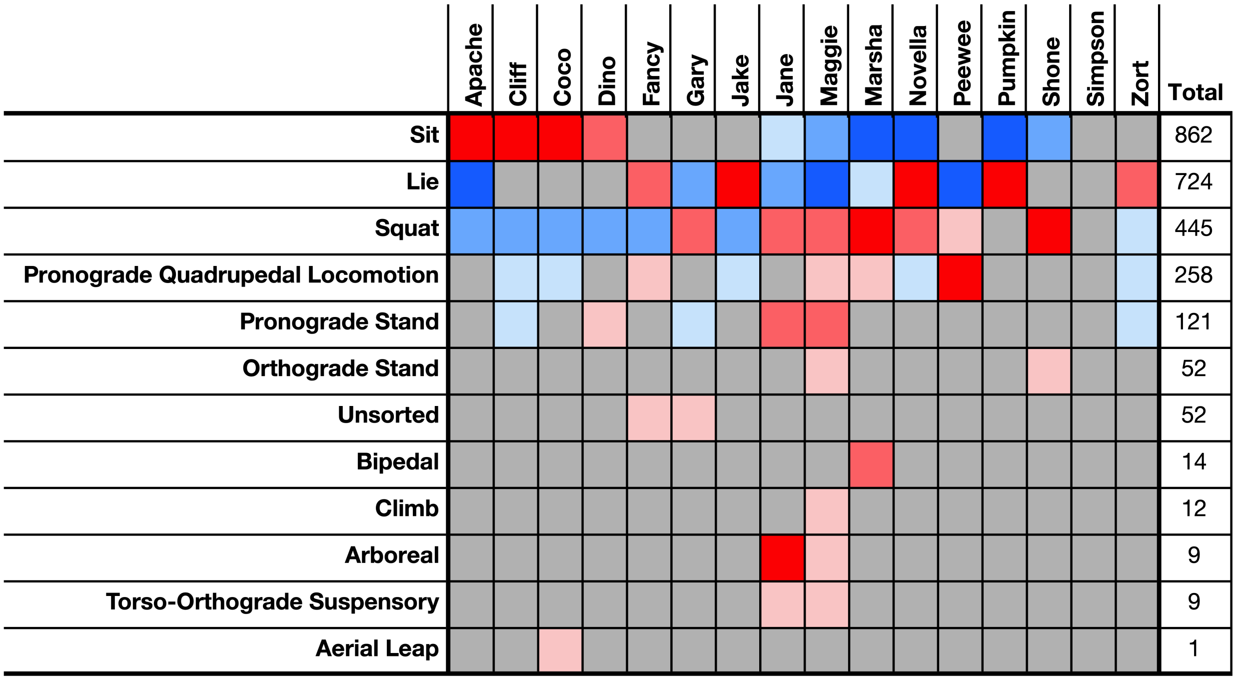


Figure 4.2.1.1 Subjects' profiles of positional behaviors under the Pos8 classification schema. Positional behavior profiles were significantly different between subjects (Chi-square = 1301, df = 165, $p < 2.2 \times 10^{-16}$). Pearson residual values were used to determine significant deviations from expected values. More intense red shading corresponds to significantly greater relative frequencies of the behavior ($p < 0.05$), while more intense blue shading corresponds to significantly lower relative frequencies of the behavior ($p < 0.05$). Actual residuals are excluded for simplicity.

Table 4.2.1.1 Sex Differences in Pos8 Behavioral Expression.

	Male	Female	Tot	% Tot	% M	% F
Sit	15.733 (727)	-15.733 (135)	862	33.69	44.88	14.38
Lie	-2.853 (427)	2.853 (297)	724	28.29	26.36	31.63
Squat	-8.626 (202)	8.626 (243)	445	17.39	12.47	25.88
Pronograde Quadrupedal Locomotion	-2.088 (148)	2.088 (110)	258	10.08	9.14	11.71
Pronograde Stand	-4.947 (51)	4.947 (70)	121	4.73	3.15	7.45
Orthograde Stand	-1.721 (27)	1.721 (25)	52	2.03	1.67	2.66
Unsorted	-2.302 (25)	2.302 (27)	52	2.03	1.54	2.88
Bipedal	-1.592 (6)	1.592 (8)	14	0.55	0.37	0.85
Climb	-1.559 (5)	1.559 (7)	12	0.47	0.31	0.75
Torso-Orthograde Suspensory	-3.255 (1)	3.255 (8)	9	0.35	0.06	0.85
Arboreal	-3.947 (0)	3.947 (9)	9	0.35	0.00	0.96
Aerial Leap	0.761 (1)	-0.761 (0)	1	0.04	0.06	0.00

Pos8 Positional behavior profiles were significantly different between subjects (Chi-square = 298.39, df = 11, $p < 2.2 \times 10^{-16}$).
Pearson residual values were used to determine significant deviations from expected values.
More intense red shading corresponds to significantly greater relative frequencies of the behavior ($p < 0.05$), while more intense blue shading corresponds to significantly lower relative frequencies of the behavior ($p < 0.05$).
% M and % F represents the percent of time engaged in the behavior by males and females, respectively.

postures, locomote by walking and by torso-orthograde suspension, and were more likely to be found lying down ($p < 0.05$).

Rates of locomotion varied by individual ($p < 2.2 \times 10^{-16}$; see Table 4.2.1.2). Cliff, Coco, Jake, and Zort demonstrated the lowest relative rates of locomotion, while Peewee, Maggie, and Marsha expressed the highest rates of locomotion. The overall rates of engaging in locomotor behaviors versus stationary postures varied by sex ($p = 0.0002543$; see Table S4.2.1.1). Overall, females tended to engage in locomotion more frequently than did males ($p < 0.05$).

Individuals also showed significant differences in their tendencies for engaging in pronograde and orthograde body orientations ($p < 2.2 \times 10^{-16}$; see Figure S4.2.1.1). Cliff and Gary were the most likely to engage in orthograde body orientations, whereas Pumpkin was the most likely to engage in pronograde body orientations ($p < 0.05$). Differences in body orientation were

Table 4.2.1.2 Percentage of Time Expressing Locomotion Versus Posture in Each Subject.

	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane
Locomotion	9.09	3.75	5.63	8.75	16.45	9.21	4.38	13.04
Posture	90.91	96.25	94.38	91.25	83.55	90.79	95.63	86.96

	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort
Locomotion	23.38	20.89	5.88	28.25	7.64	11.39	13.55	5.03
Posture	76.62	79.11	94.12	71.75	92.36	88.61	86.45	94.97

Significantly different rates of locomotion versus stationary postures were recorded depending on the identity of the subject (Chi-square = 164.27, df = 30, $p < 2.2 \times 10^{-16}$).
Cells contain the observed percent of time the subject engaged in the behavior.
Cell shadings are derived from Pearson residuals.
See Table 4.2.1.1 for description of cell shading.

observed according to sex ($p < 1.466 \times 10^{-10}$; see Table S4.2.1.2). Males were more likely to engage in orthograde body orientations, whereas females were more likely to engage in pronograde body orientations ($p < 0.05$).

Considering the Pos7 categorization schema provides a slightly more detailed look at the individual differences in positional behaviors throughout the study ($p < 2.2 \times 10^{-16}$; see Table S4.2.1.2). These included differences in individuals’ rates of squatting on only one heel and individual tendencies for the means of lying down. Female chimpanzees were more likely to squat on one heel, and were more likely to lie on their fronts and the combination of their side and back ($p < 0.05$; see Table S4.2.1.3).

Figure 4.2.1.2 highlights the difference between individuals according to the positional categories proposed in Hunt (1996) ($p < 2.2 \times 10^{-16}$). Sex differences were observed for the expression of behaviors falling under the positional categories of Pos4 ($p < 2.2 \times 10^{-16}$; see Table S4.2.1.3) Under these categories, males were more likely to engage in the Sit-Out, Chair-Sit, and Sit-In/Out postures, while females were more likely to engage in positional modes like Squatting, Supine Lie, and Forelimb-Suspend Squat ($p < 0.05$).

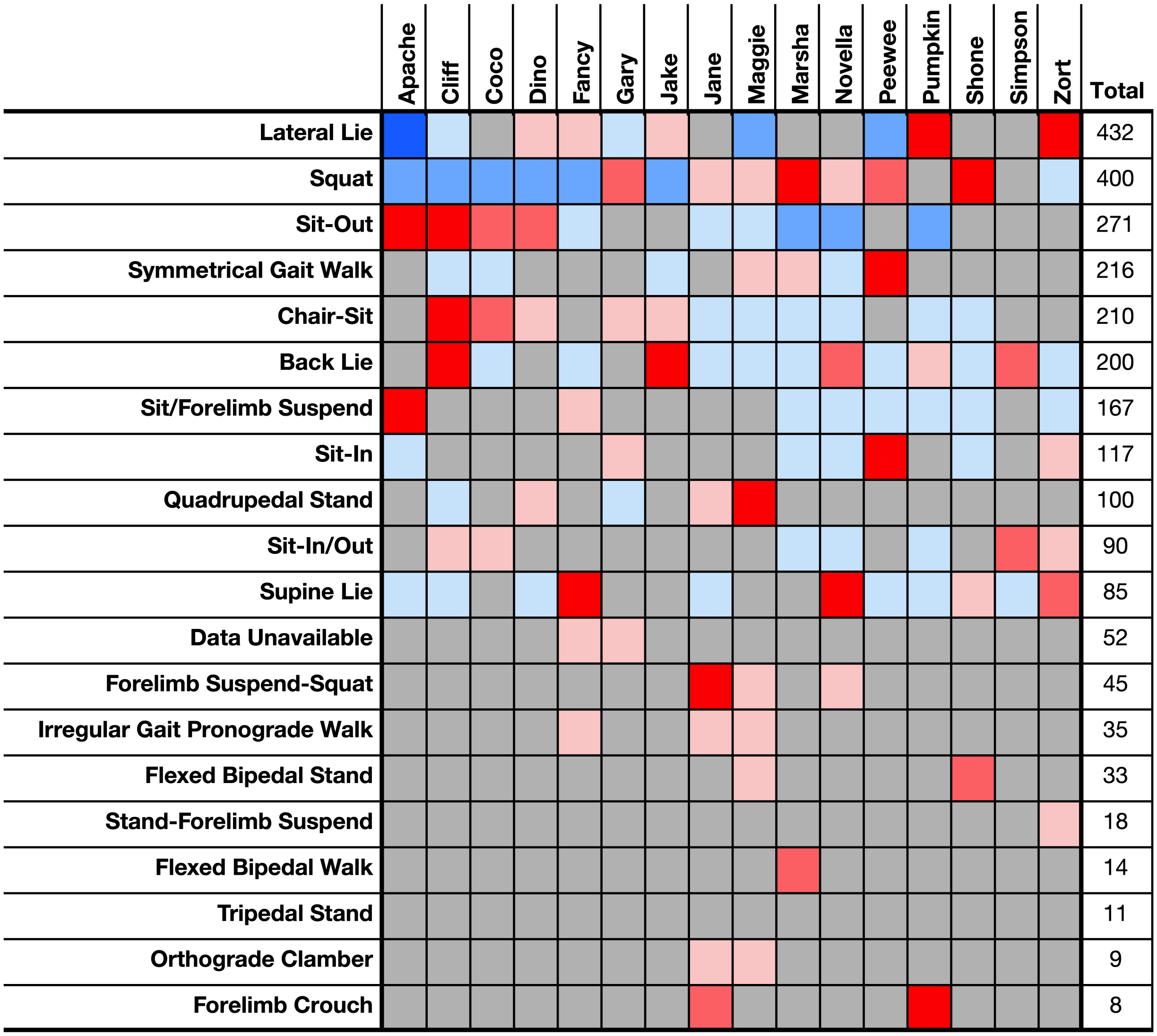
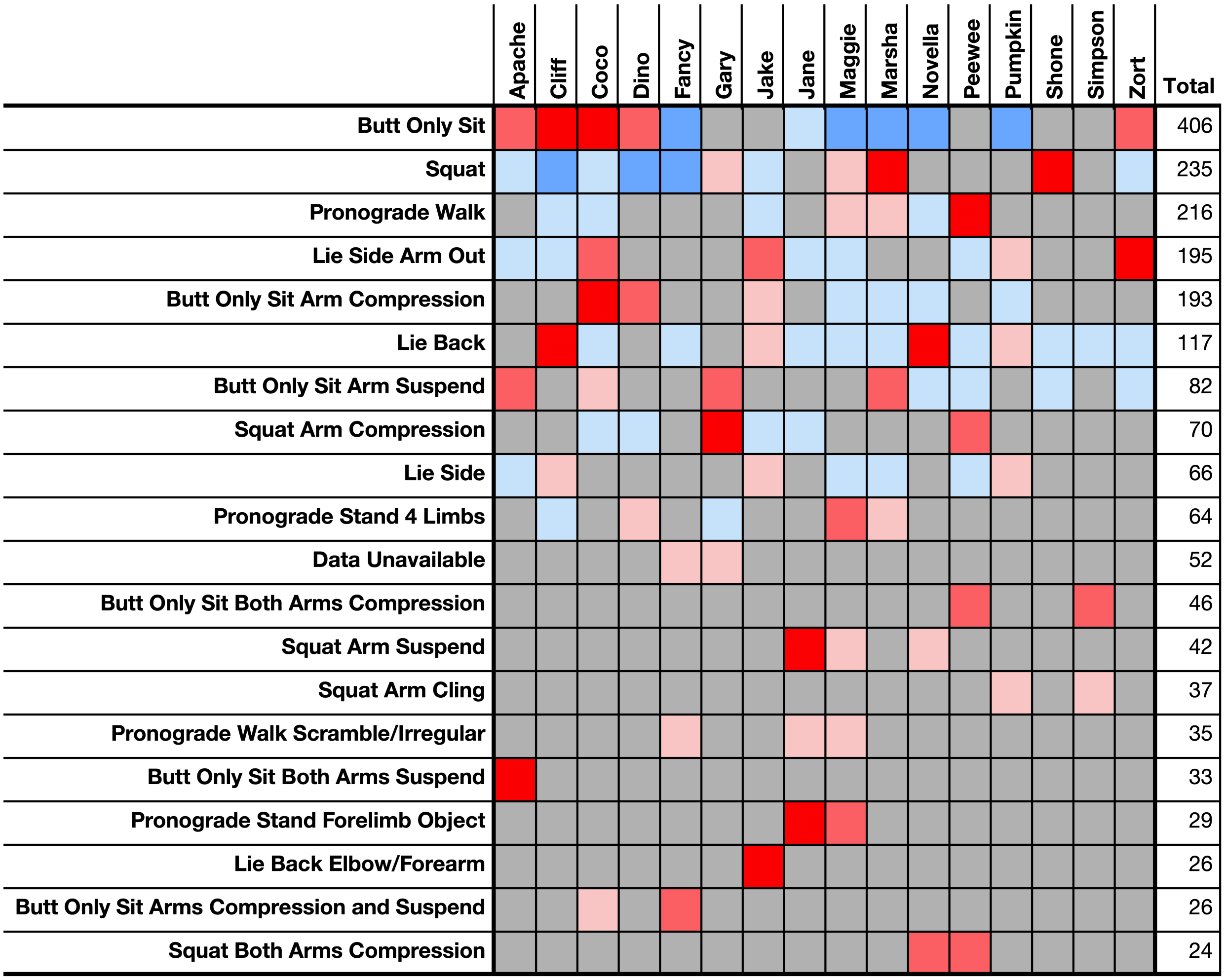


Figure 4.2.1.2 Subjects' profiles of positional behaviors under the Pos4 classification schema. Positional behavior profiles were significantly different between subjects (Chi-square = 2383.3, df = 480, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

Figure 4.2.1.3 shows the individual differences in expression of behaviors under the Pos3 categorization schema ($p < 2.2 \times 10^{-16}$). Table S4.2.1.5 shows the sex difference in behaviors according to Pos3 ($p < 2.2 \times 10^{-16}$). Individual differences in expression of the Pos1 positional behavior categories can be seen in Figure S4.2.1.3 ($p < 2.2 \times 10^{-16}$).



	Total
Butt Only Sit	406
Squat	235
Pronograde Walk	216
Lie Side Arm Out	195
Butt Only Sit Arm Compression	193
Lie Back	117
Butt Only Sit Arm Suspend	82
Squat Arm Compression	70
Lie Side	66
Pronograde Stand 4 Limbs	64
Data Unavailable	52
Butt Only Sit Both Arms Compression	46
Squat Arm Suspend	42
Squat Arm Cling	37
Pronograde Walk Scramble/Irregular	35
Butt Only Sit Both Arms Suspend	33
Pronograde Stand Forelimb Object	29
Lie Back Elbow/Forearm	26
Butt Only Sit Arms Compression and Suspend	26
Squat Both Arms Compression	24

Figure 4.2.1.3 Subjects' profiles of positional behaviors under the Pos3 classification schema. Positional behavior profiles were significantly different between subjects (Chi-square = 6945.5, df = 2265, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

The Positional behaviors expressed by the group changed after the installation of the climbing aid and the group's return to their typical enclosure (see Table 4.2.1.3 for changes to Pos4; $p < 9.402 \times 10^{-15}$) Sit-In, Chair Sit, and Back Lie were less frequent after the installation of the climbing aid, while Supine Lie, Sit-Out, and Flexed Bipedal Walk occurred more frequently ($p < 0.05$). Changes in positional behavior expression also occurred between the two periods of the study according to the Pos3 categorization schema ($p < 2.2 \times 10^{-16}$; see Table S4.2.1.6). This change was associated with an increase in lying on one's limbs, lying on one's side, and engaging in bipedal locomotion ($p < 0.05$). Rates of stationary orthograde standing decreased after the group's return ($p < 0.05$). Rates of locomotion and engaging in stationary postures were not significantly different between the periods before and after the installation of the climbing aid ($p = 0.1079$; see Table S4.2.1.7).

4.2.2 Limb and Body Element Engagement

Table 4.2.1.3 Differences in Pos 4 Behavioral Expression by Study Period.

	Before	After	Total	% Total	% Before	% After
Lateral Lie	-1.574 (201)	1.574 (231)	432	16.88	15.72	18.05
Squat	-0.318 (197)	0.318 (203)	400	15.63	15.40	15.86
Sit-Out	-2.884 (113)	2.884 (158)	271	10.59	8.84	12.34
Symmetrical Gait Walk	-1.701 (96)	1.701 (120)	216	8.44	7.51	9.38
Chair-Sit	3.175 (127)	-3.175 (83)	210	8.21	9.93	6.48
Back Lie	2.215 (115)	-2.215 (85)	200	7.82	8.99	6.64
Sit/Forelimb Suspend	-1.035 (77)	1.035 (90)	167	6.53	6.02	7.03
Sit-In	5.777 (89)	-5.777 (28)	117	4.57	6.96	2.19
Quadrupedal Stand	0.208 (51)	-0.208 (49)	100	3.91	3.99	3.83
Sit-In/Out	-0.211 (44)	0.211 (46)	90	3.52	3.44	3.59
Supine Lie	-4.519 (22)	4.519 (63)	85	3.32	1.72	4.92
Data Unavailable	4.766 (43)	-4.766 (9)	52	2.03	3.36	0.70
Forelimb Suspend-Squat	-1.351 (18)	1.351 (27)	45	1.76	1.41	2.11
Irregular Gait Pronograde Walk	0.173 (18)	-0.173 (17)	35	1.37	1.41	1.33
Flexed Bipedal Stand	1.229 (20)	-1.229 (13)	33	1.29	1.56	1.02
Stand-Forelimb Suspend	1.894 (13)	-1.894 (5)	18	0.70	1.02	0.39
Flexed Bipedal Walk	-2.142 (3)	2.142 (11)	14	0.55	0.23	0.86
Tripedal Stand	-0.905 (4)	0.905 (7)	11	0.43	0.31	0.55
Orthograde Clamber	-1.001 (3)	1.001 (6)	9	0.35	0.23	0.47
Forelimb Crouch	1.418 (6)	-1.418 (2)	8	0.31	0.47	0.16

Positional behavior profiles under the Pos4 classification schema were significantly different between the two study periods (Chi-square = 135.83, df = 32, p < 9.402 x10^{-15}).
See Table 4.2.1.1 for description of cell contents, and shading.
Only the first 20 rows are displayed.

Tendencies for limb engagement, combined engagement of limbs, and engagement of one's axial body varied by individual according to multiple metrics. Use of a given forelimb varied by individual ($p < 2.2 \times 10^{-16}$; see Figure 4.2.2.1). Apache and Zort showed the highest rates of arm contact without bearing weight. Apache, Jane and Fancy displayed arm suspension most frequently ($p < 0.05$). Cliff and Novella displayed the highest rates of self-clasping ($p < 0.05$). Gary was the most likely to fail to operate his arms to fit any defined category ($p < 0.05$). PeeWee and Maggie bore weight on their arms via compression ($p < 0.05$). Maggie and Jane showed the highest rates of clinging with their arms ($p < 0.05$). Arms were laid out most frequently by Zort, Simpson, and Pumpkin. Pumpkin and Cliff were the individuals most likely to engage their arms in object manipulation ($p < 0.05$). The chimpanzees who engaged their

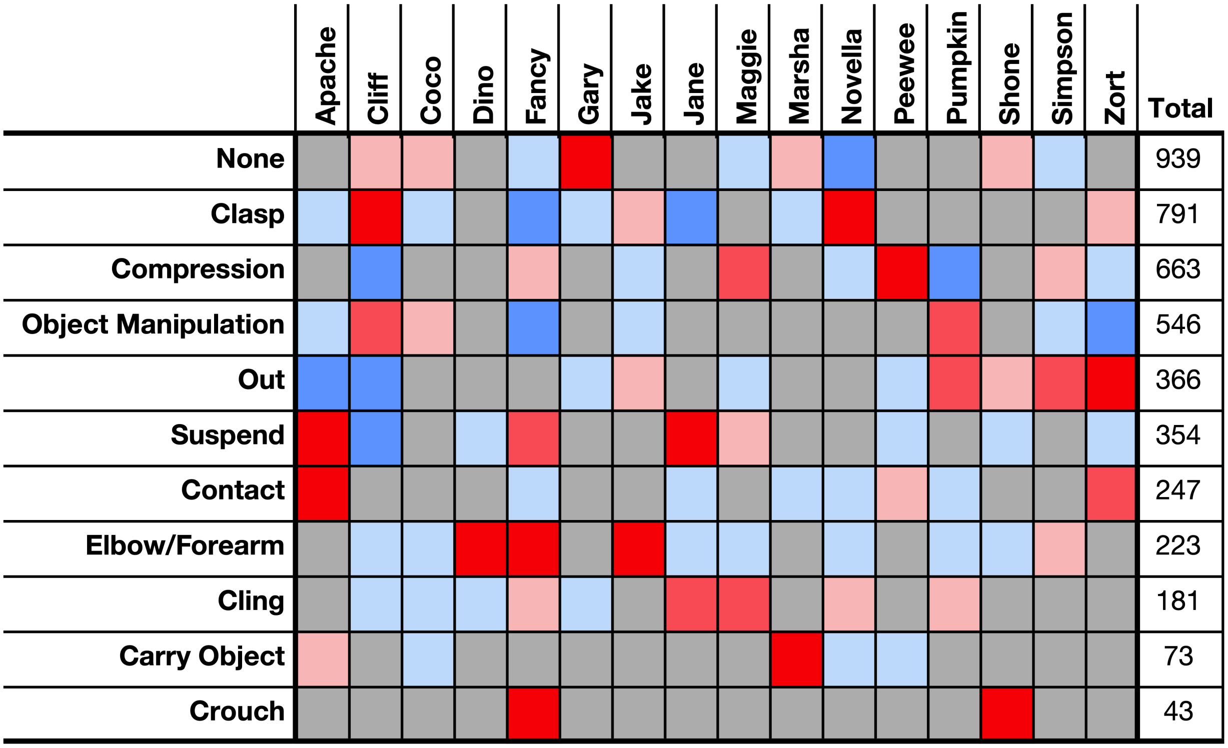


Figure 4.2.2.1 The tendencies for engagement of a given forelimb were significantly different between subjects (Chi-square = 1657.3, df = 150, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

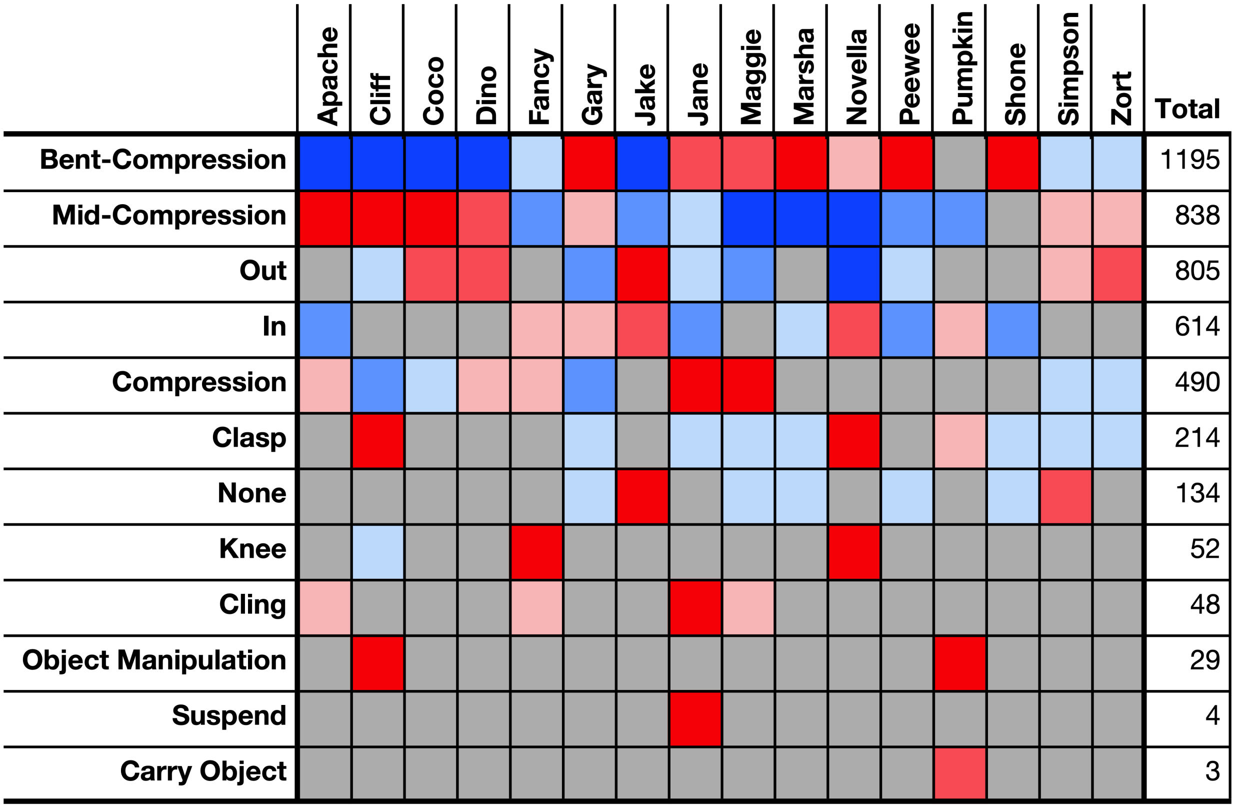
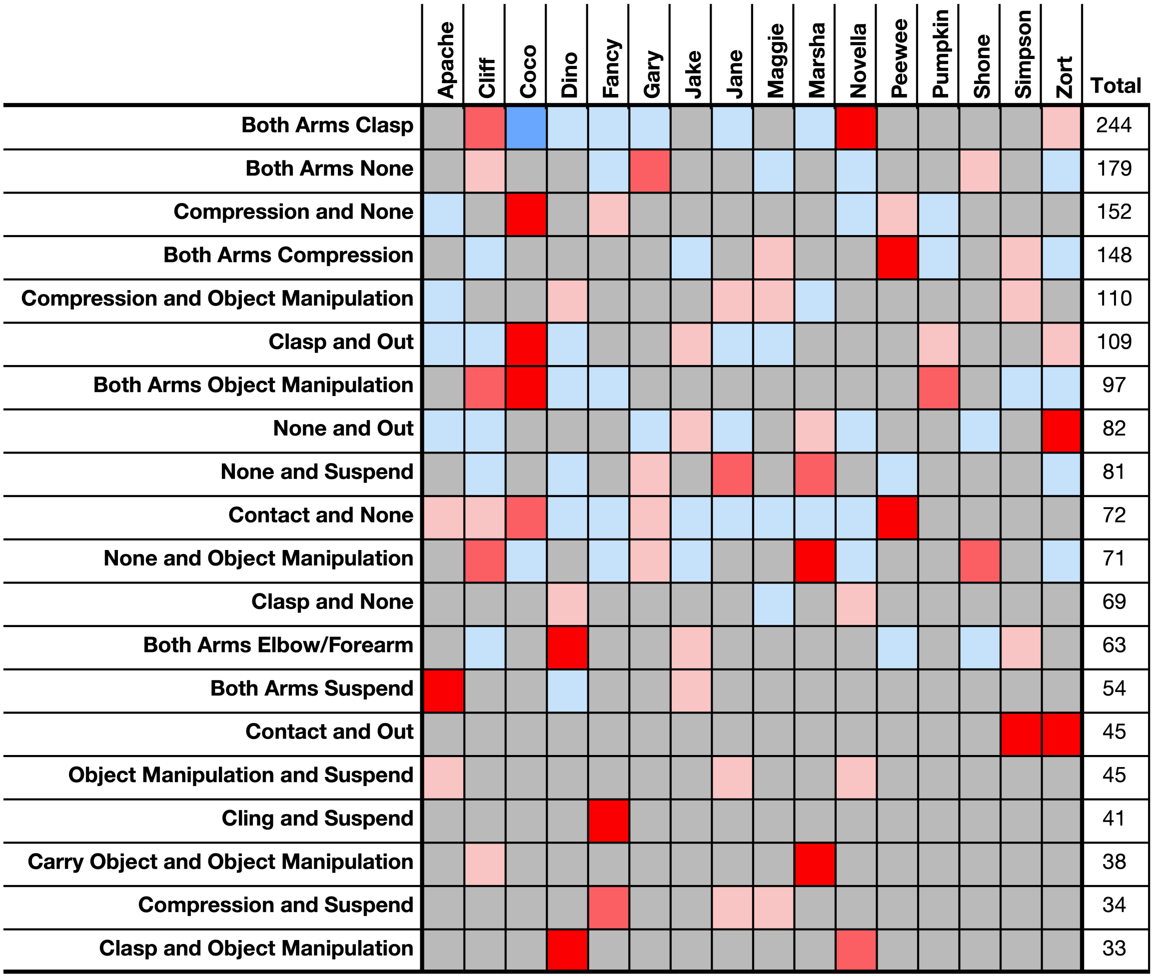


Figure 4.2.2.2 The tendencies for engagement of a given hindlimb were significantly different between subjects (Chi-square = 2452.7, df = 165, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

elbows or forearms with their environment most often were Dino, Fancy, and Jake ($p < 0.05$). Fancy and Shone were the chimpanzees most likely to engage their arms in the crouched position ($p < 0.05$).

Hindlimb use also varied by individual ($p < 2.2 \times 10^{-16}$; see Figure 4.2.2.2). Engaging one's leg in the bent-compression state was most common for Gary, Marsha, Peewee, Shone, Jane, and Maggie ($p < 0.05$). Apache, Cliff, Coco, and Dino were the chimpanzees most likely to engage their legs in the mid-compression state ($p < 0.05$). Jake, Coco, Dino, and Zort displayed the highest rates of laying their legs out. Jake and Novella were the individuals most likely to lay their legs in ($p < 0.05$). Jane and Maggie engaged their legs in basic compression most frequently

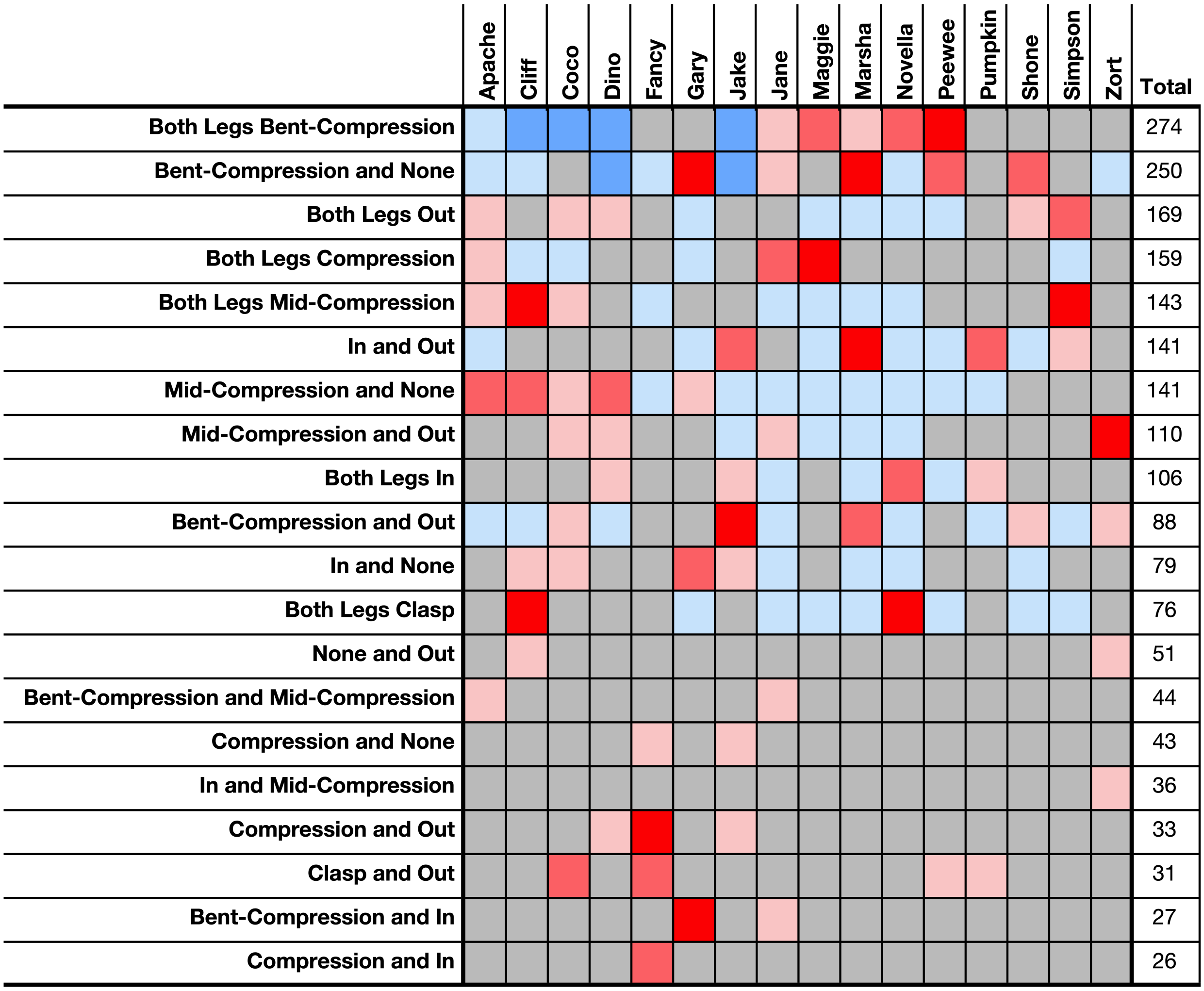


	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort	Total
Both Arms Clasp																	244
Both Arms None																	179
Compression and None																	152
Both Arms Compression																	148
Compression and Object Manipulation																	110
Clasp and Out																	109
Both Arms Object Manipulation																	97
None and Out																	82
None and Suspend																	81
Contact and None																	72
None and Object Manipulation																	71
Clasp and None																	69
Both Arms Elbow/Forearm																	63
Both Arms Suspend																	54
Contact and Out																	45
Object Manipulation and Suspend																	45
Cling and Suspend																	41
Carry Object and Object Manipulation																	38
Compression and Suspend																	34
Clasp and Object Manipulation																	33

Figure 4.2.2.3 The tendencies for simultaneous forelimb engagements were significantly different between subjects (Chi-square = 3546.7, df = 840, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

($p < 0.05$). Cliff and Novella were the most likely to engage in hindlimb self-clasping ($p < 0.05$). Jake and Simpson were the most likely to fail to engage their legs with their environment on any given scan. Fancy and Novella rested weight on their knees at the highest rates ($p < 0.05$).

Additional motifs for limb use combinations were observed to vary by subject identity. Individual differences ($p < 2.2 \times 10^{-16}$) in the simultaneous engagement of one's forelimbs can be found in Figure 4.2.2.3. Novella and Cliff were the individuals most likely to clasp their body with both of their arms. Peewee was the most likely to bear weight on both of his forelimbs in a



	Total
Both Legs Bent-Compression	274
Bent-Compression and None	250
Both Legs Out	169
Both Legs Compression	159
Both Legs Mid-Compression	143
In and Out	141
Mid-Compression and None	141
Mid-Compression and Out	110
Both Legs In	106
Bent-Compression and Out	88
In and None	79
Both Legs Clasp	76
None and Out	51
Bent-Compression and Mid-Compression	44
Compression and None	43
In and Mid-Compression	36
Compression and Out	33
Clasp and Out	31
Bent-Compression and In	27
Compression and In	26

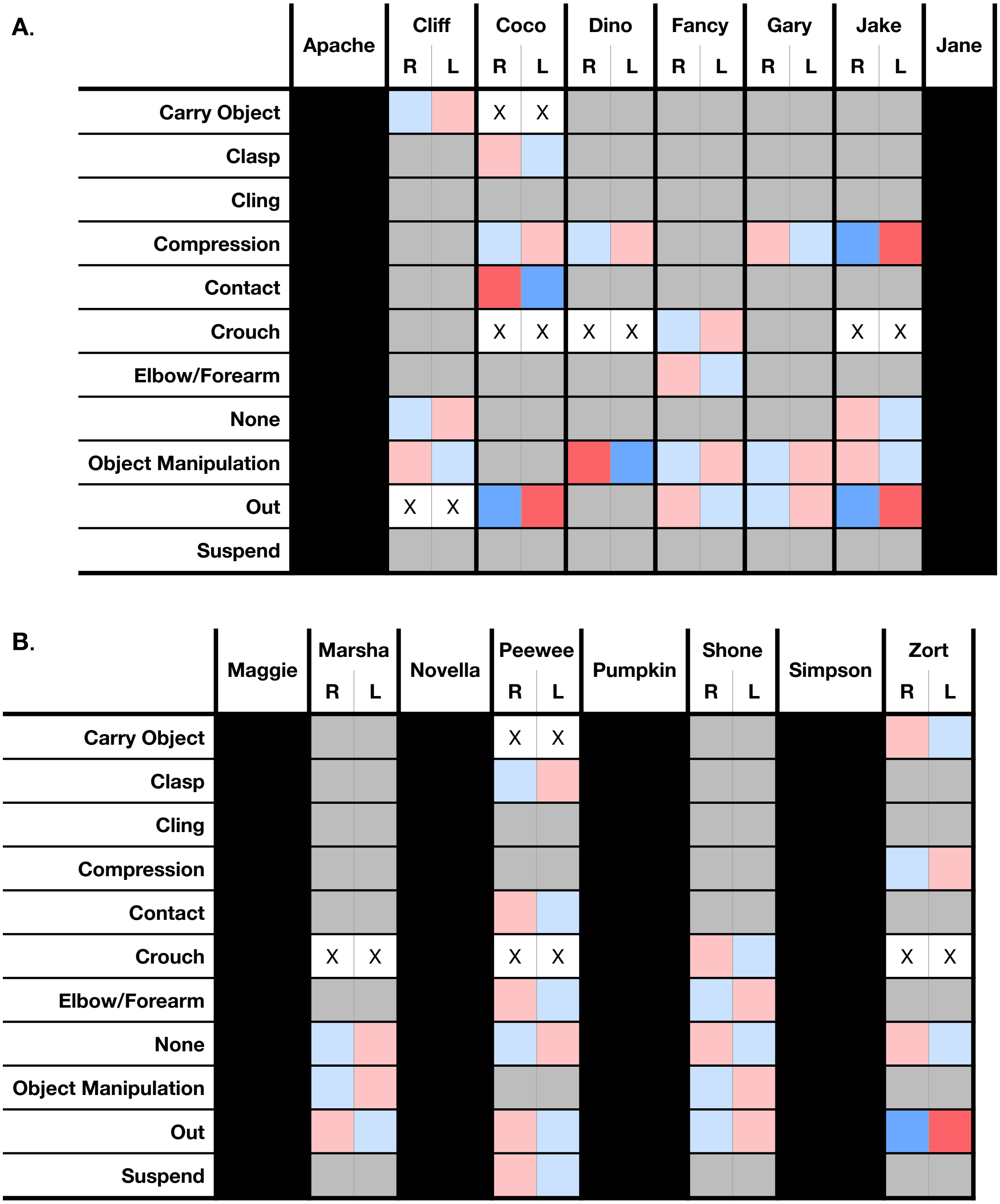
Figure 4.2.2.4 The types of simultaneous hindlimb engagements were significantly different between subjects (Chi-square = 3444.9, df = 705, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

compressive manner. Dino was the subject most commonly seen simultaneously leaning on both of his elbows/forearms. Tendencies for the simultaneous engagement of one's hindlimbs also varied by individual ($p < 2.2 \times 10^{-16}$; see Figure 4.2.2.4). Peewee, Maggie, and Novella were the chimpanzees most likely to engage both legs in the bent-compression mode. Jake and Novella were the most likely to engage one leg in the bent-compression position and the other resting out on a substrate. Cliff and Simpson were the chimpanzees most commonly seen with both legs in the mid-compression state. Relative rates of positional motifs related to the simultaneous engagement of ipsilateral limbs is represented in Figure S4.2.2.1 ($p < 2.2 \times 10^{-16}$), while contralateral limb engagement motifs are represented in Figure S4.2.2.2 ($p < 2.2 \times 10^{-16}$).

The tendencies for individuals to engage either particular arm or leg in the manners specified in the ethogram are displayed in Figure S4.2.2.3 and Figure S4.2.2.4, respectively. The relative frequencies at which each subject leaned against a substrate using combinations of their head and torso are presented in Figure S4.2.2.5 ($p < 2.2 \times 10^{-16}$).

Finally, differences in limb use tendency differed by body side (left versus right) for many subjects ($p < 0.05$). Forelimb sidedness is presented in Figure 4.2.2.5, while hindlimb sidedness is presented in Figure 4.2.2.6. Cliff, Coco, Dino, Fancy, Gary, Jake, Marsha, Peewee, Shone, and Zort showed differences in their use of each forelimb ($p < 0.05$). Coco, Jake and Zort all rested their left arms in the “Out” position significantly more often than their right arms. Jake was more likely to engage his left arm in compression than his right. Dino was more likely to manipulate objects with his right hand than his left. Coco was more likely to maintain contact with a substrate with his right hand without bearing significant weight upon it. Several additional differences in use between the two arms were significant, but less severe. Sidedness in hindlimb use was displayed by Apache, Coco, Jake, Jane, Marsha, Novella, Peewee, Shone, Simpson, and Zort ($p < 0.05$). Among the larger side-dependent differences was Jake’s tendency to position his right leg in the bent-compression state more often than his left leg. Both Marsha and Simpson rested their right leg in more often than their left. Novella leaned on her left knee more than her right, Simpson failed to engage his left leg with his surroundings more frequently than he failed to engage his right leg, and Zort rested his left leg out more often than his right leg.

4.2.3 Positional Diversity



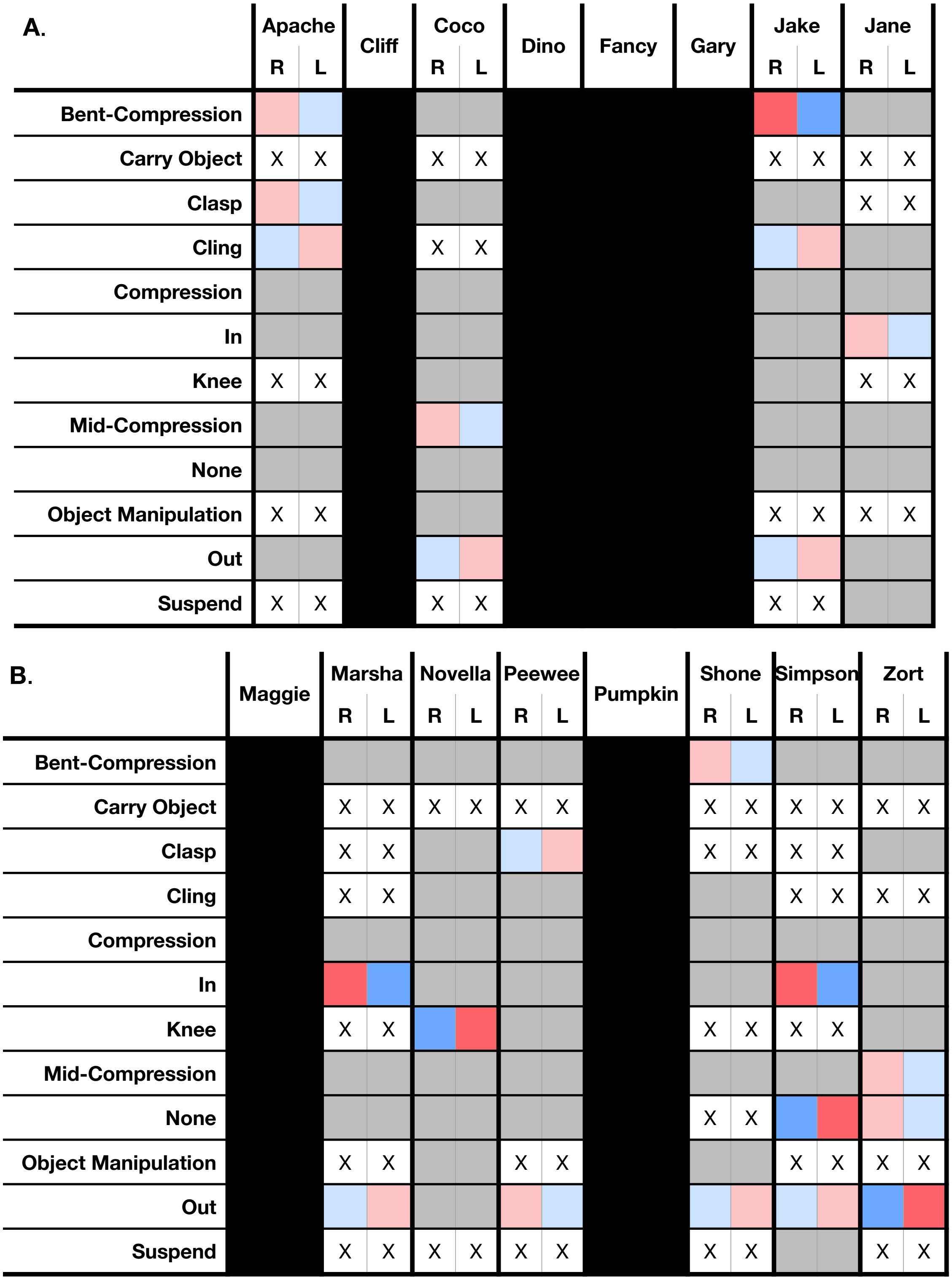
A.

	Apache	Cliff		Coco		Dino		Fancy		Gary		Jake		Jane
		R	L	R	L	R	L	R	L	R	L	R	L	
Carry Object				X	X									
Clasp														
Cling														
Compression														
Contact														
Crouch				X	X	X	X					X	X	
Elbow/Forearm														
None														
Object Manipulation														
Out		X	X											
Suspend														

B.

	Maggie	Marsha		Novella	Peewee		Pumpkin	Shone		Simpson	Zort	
		R	L		R	L		R	L		R	L
Carry Object					X	X						
Clasp												
Cling												
Compression												
Contact												
Crouch		X	X		X	X					X	X
Elbow/Forearm												
None												
Object Manipulation												
Out												
Suspend												

Figure 4.2.2.5 The tendencies for engagement of forelimbs were significantly different between the right and left sides for highlighted individuals ($p < 0.05$). **A.** Includes Apache, Cliff, Coco, Dino, Fancy, Gary, Jake, and Jane. **B.** Includes Maggie, Marsha, Novella, Peewee, Pumpkin, Shone, Simpson, and Zort. See Figure 4.2.1.1 for description of cell shading. An "X" denotes that the behavior was not observed. Black shaded cells signify that the subject did not exhibit significant sidedness overall ($p < 0.05$).



A.

	Apache		Cliff	Coco		Dino	Fancy	Gary	Jake		Jane	
	R	L		R	L				R	L	R	L
Bent-Compression	🩷	🩵	■	▨	▨	■	■	■	🟥	🟦	▨	▨
Carry Object	X	X	■	X	X	■	■	■	X	X	X	X
Clasp	🩷	🩵	■	▨	▨	■	■	■	▨	▨	X	X
Cling	🩵	🩷	■	X	X	■	■	■	🩵	🩷	▨	▨
Compression	▨	▨	■	▨	▨	■	■	■	▨	▨	▨	▨
In	▨	▨	■	▨	▨	■	■	■	▨	▨	🩷	🩵
Knee	X	X	■	▨	▨	■	■	■	▨	▨	X	X
Mid-Compression	▨	▨	■	🩷	🩵	■	■	■	▨	▨	▨	▨
None	▨	▨	■	▨	▨	■	■	■	▨	▨	▨	▨
Object Manipulation	X	X	■	▨	▨	■	■	■	X	X	X	X
Out	▨	▨	■	🩵	🩷	■	■	■	🩵	🩷	▨	▨
Suspend	X	X	■	X	X	■	■	■	X	X	▨	▨

B.

	Maggie	Marsha		Novella		Peewee		Pumpkin	Shone		Simpson		Zort	
		R	L	R	L	R	L		R	L	R	L	R	L
Bent-Compression	■	▨	▨	▨	▨	▨	▨	■	🩷	🩵	▨	▨	▨	▨
Carry Object	■	X	X	X	X	X	X	■	X	X	X	X	X	X
Clasp	■	X	X	▨	▨	🩵	🩷	■	X	X	X	X	▨	▨
Cling	■	X	X	▨	▨	▨	▨	■	▨	▨	X	X	X	X
Compression	■	▨	▨	▨	▨	▨	▨	■	▨	▨	▨	▨	▨	▨
In	■	🟥	🟦	▨	▨	▨	▨	■	▨	▨	🟥	🟦	▨	▨
Knee	■	X	X	🟦	🟥	▨	▨	■	X	X	X	X	▨	▨
Mid-Compression	■	▨	▨	▨	▨	▨	▨	■	▨	▨	▨	▨	🩷	🩵
None	■	▨	▨	▨	▨	▨	▨	■	X	X	🟦	🟥	🩷	🩵
Object Manipulation	■	X	X	▨	▨	X	X	■	▨	▨	X	X	X	X
Out	■	🩵	🩷	▨	▨	🩷	🩵	■	🩵	🩷	🩵	🩷	🟦	🟥
Suspend	■	X	X	X	X	X	X	■	X	X	▨	▨	X	X

Figure 4.2.2.6 The tendencies for engagement of hindlimbs were significantly different between the right and left sides for highlighted individuals ($p < 0.05$). **A.** Includes Apache, Cliff, Coco, Dino, Fancy, Gary, Jake, and Jane. **B.** Includes Maggie, Marsha, Novella, Peewee, Pumpkin, Shone, Simpson, and Zort. See Figure 4.2.1.1 for description of cell shading. An "X" denotes that the behavior was not observed. Black shaded cells signify that the subject did not exhibit significant sidedness overall ($p < 0.05$).

The diversity of positional behaviors and their evenness for each subject under the most detailed positional classification schema, Pos1, is represented in Table 4.2.3.1. Additional positional diversity scores were calculated using the alternative classification schemas, Pos2-8 (see Table 4.2.3.2). Table 4.2.3.3 shows the positional diversity under the Pos1 schema for individuals overall, as well as solely among their postures, locomotion, sitting and squatting

Table 4.2.3.1 Individual Positional Diversity and Evenness Indices Under Pos1.

	Pos1	
	H	**(J)**
Apache	**3.71**	0.91
Cliff	**3.01**	0.80
Coco	**3.71**	0.90
Dino	**3.57**	0.89
Fancy	**3.91**	0.91
Gary	**3.52**	0.86
Jake	**3.98**	0.94
Jane	**3.81**	0.93
Maggie	**3.66**	0.88
Marsha	**3.26**	0.87
Novella	**3.66**	0.88
Peewee	**3.41**	0.83
Pumpkin	**4.07**	0.93
Shone	**3.33**	0.86
Simpson	**3.73**	0.90
Zort	**3.82**	0.93
Mean	**3.64**	0.89

Shannon diversity index (H) and species evenness (J) calculated according to each individual's overall expressed rates of positional behaviors under the Pos1 classification schema.
Light red or light blue shading signify that scores are within one standard deviation above and below the mean respectively. Each increase in intensity of red and blue shading signifies that the score falls outside of an additional standard deviation from the mean.
The same coloring convention applies to the text color of the evenness scores.

postures, and lying postures. Notably, Cliff demonstrated the lowest positional diversity scores for all positional categorization schemas but Pos5, for which he had the second lowest positional diversity score. His positional diversity was outside of two standard deviations from the mean under Pos1 overall and for all postures, whereas his diversity was within two standard deviations from the mean for lying and the combined sitting and squatting category. Cliff's locomotor diversity was within one standard deviation from the mean. Pumpkin, Jake and Fancy had the

Table 4.2.3.2 Individual Diversity and Evenness Indices Under Multiple Positional Classification Schemas

	Pos1		**Pos2**		**Pos3**		**Pos4**		**Pos5**		**Pos6**		**Pos7**		**Pos8**	
	H	**(J)**	**H**	**(J)**	**H**	**(J)**	**H**	**(J)**	**H**	**(J)**	**H**	**(J)**	**H**	**(J)**	**H**	**(J)**
Apache	**3.71**	0.91	**3.67**	0.91	**2.62**	0.78	**2.10**	0.78	**2.76**	0.87	**2.52**	0.80	**1.22**	0.53	**1.13**	0.58
Cliff	**3.01**	0.80	**2.81**	0.78	**1.63**	0.60	**1.88**	0.76	**2.29**	0.73	**1.48**	0.56	**1.01**	0.52	**0.84**	0.47
Coco	**3.71**	0.90	**3.44**	0.86	**2.17**	0.67	**2.14**	0.76	**2.75**	0.81	**2.04**	0.67	**1.28**	0.48	**1.06**	0.48
Dino	**3.57**	0.89	**3.41**	0.88	**2.59**	0.78	**2.12**	0.78	**2.66**	0.84	**2.34**	0.80	**1.62**	0.68	**1.21**	0.62
Fancy	**3.91**	0.91	**3.76**	0.90	**3.31**	0.87	**2.37**	0.82	**3.02**	0.87	**3.02**	0.87	**2.07**	0.78	**1.45**	0.66
Gary	**3.52**	0.86	**3.40**	0.86	**2.57**	0.79	**2.23**	0.81	**2.57**	0.80	**2.51**	0.80	**1.81**	0.73	**1.47**	0.76
Jake	**3.98**	0.94	**3.80**	0.93	**2.65**	0.83	**1.99**	0.78	**3.06**	0.89	**2.43**	0.81	**1.44**	0.69	**0.96**	0.60
Jane	**3.81**	0.93	**3.68**	0.92	**3.35**	0.90	**2.54**	0.85	**2.83**	0.83	**3.28**	0.90	**2.22**	0.87	**1.86**	0.81
Maggie	**3.66**	0.88	**3.48**	0.86	**3.24**	0.87	**2.57**	0.82	**2.59**	0.76	**3.17**	0.88	**2.32**	0.82	**1.95**	0.81
Marsha	**3.26**	0.87	**2.84**	0.83	**2.54**	0.77	**1.96**	0.71	**2.09**	0.72	**2.39**	0.77	**2.25**	0.81	**1.67**	0.72
Novella	**3.66**	0.88	**3.31**	0.84	**2.98**	0.83	**2.13**	0.73	**2.43**	0.75	**2.53**	0.72	**2.25**	0.81	**1.36**	0.59
Peewee	**3.41**	0.83	**3.20**	0.81	**2.55**	0.78	**2.07**	0.77	**2.31**	0.72	**2.55**	0.79	**1.80**	0.70	**1.49**	0.72
Pumpkin	**4.07**	0.93	**3.57**	0.88	**3.14**	0.84	**1.95**	0.70	**2.65**	0.82	**2.67**	0.77	**2.05**	0.80	**1.31**	0.63
Shone	**3.33**	0.86	**3.14**	0.82	**2.70**	0.78	**2.15**	0.76	**2.40**	0.76	**2.63**	0.78	**2.10**	0.82	**1.71**	0.74
Simpson	**3.73**	0.90	**3.57**	0.88	**2.84**	0.86	**2.39**	0.86	**2.80**	0.83	**2.81**	0.86	**1.86**	0.73	**1.52**	0.73
Zort	**3.82**	0.93	**3.55**	0.90	**2.43**	0.76	**2.18**	0.79	**2.98**	0.90	**2.01**	0.68	**1.81**	0.73	**1.25**	0.64
Mean	**3.64**	0.89	**3.41**	0.87	**2.71**	0.79	**2.17**	0.78	**2.64**	0.81	**2.52**	0.78	**1.82**	0.72	**1.39**	0.66

Shannon diversity index (H) and species evenness (J) calculated according to each individual's overall expressed rates of positional behaviors under each of the eight categorization schemas: Pos1, Pos2, Pos3, Pos4, Pos5, Pos6, Pos7, and Pos8.
See Table 4.2.3.1 for description of cell shading and text coloring.

Table 4.2.3.3 Pos1 Positional Diversity for Broad Positional Modes

	All		Postures		Locomotion		Sit and Squat		Lie	
	H	(J)	H	(J)	H	(J)	H	(J)	H	(J)
Apache	3.71	0.91	3.65	0.91	0.76	0.69	3.43	0.90	1.38	0.86
Cliff	3.01	0.80	2.94	0.79	0.45	0.65	2.70	0.77	1.41	0.79
Coco	3.71	0.90	3.61	0.89	1.58	0.88	3.30	0.89	1.91	0.77
Dino	3.57	0.89	3.52	0.89	0.75	0.54	2.83	0.86	2.66	0.87
Fancy	3.91	0.91	4.02	0.95	0.66	0.60	3.27	0.96	3.28	0.92
Gary	3.52	0.86	3.46	0.86	0.51	0.46	3.09	0.83	2.34	0.91
Jake	3.98	0.94	3.95	0.94	0.68	0.99	3.05	0.92	3.35	0.93
Jane	3.81	0.93	3.73	0.93	1.19	0.86	3.26	0.92	1.96	0.94
Maggie	3.66	0.88	3.66	0.91	1.24	0.64	3.35	0.91	1.75	0.98
Marsha	3.26	0.87	3.15	0.88	1.09	0.61	2.56	0.85	2.09	0.87
Novella	3.66	0.88	3.53	0.87	1.58	0.88	3.02	0.91	2.50	0.81
Peewee	3.41	0.83	3.75	0.92	0.32	0.29	3.53	0.92	1.68	0.94
Pumpkin	4.07	0.93	4.07	0.93	0.29	0.41	2.91	0.91	3.51	0.93
Shone	3.33	0.86	3.20	0.86	0.96	0.60	2.59	0.80	1.87	0.85
Simpson	3.73	0.90	3.73	0.91	0.68	0.49	3.27	0.89	2.57	0.93
Zort	3.82	0.93	3.80	0.93	0.00	N/A	3.25	0.93	2.78	0.91
Mean	3.64	0.89	3.61	0.90	0.80	0.64	3.09	0.88	2.31	0.89

Shannon diversity index (H) and species evenness (J) calculated according to each individual's expressed rates of positional behaviors under the Pos1 categorization schema overall and for each of the four indicated broad positional modes.
See Table 4.2.3.1 for description of cell shading and text coloring.

highest positional diversity values overall under Pos1 due to their high positional diversity while lying down. Apache and Cliff demonstrated the lowest values for lying diversity. Peewee and Apache demonstrated the highest diversity scores under the sitting and squatting category of Pos1, while Cliff, Marsha, and Shone had the lowest diversity values for this category. Coco and Novella demonstrated the highest locomotor diversity in this study, whereas Zort, who was not observed locomoting in any scan, had the lowest locomotor diversity score.

Table S4.2.3.1 shows the diversity scores for each individual's engagement of each of their four limbs. The lowest diversity score for use of the right arm belonged to Cliff, while the highest was attributed to Marsha. Use of the left arm had the lowest diversity score for PeeWee and was highest for Fancy and Simpson. Diversity of use for the right leg was highest in Fancy, Jake, and Pumpkin, and was lowest for PeeWee. Left leg use diversity was highest for Fancy, Novella, and Pumpkin, but lowest for Marsha.

Individuals' diversity scores for the pooled use of arms, legs, and limbs overall are portrayed in Table S4.2.3.2. Diversity of limb use combinations are reported for ipsilateral limb use combinations, contralateral limb use combinations, simultaneous engagement of both forelimbs, and simultaneous engagement of both hindlimbs (see Table S4.2.3.3). The diversity scores for pooled forelimbs were highest for Fancy, Pumpkin, and Simpson. Forelimb use diversity was lowest for Cliff, Novella, and Peewee. Pooled leg use diversity scores were highest for Fancy and Pumpkin, but lowest for Marsha, PeeWee and Gary. Overall limb use diversity was highest for Fancy and Pumpkin, but lowest for PeeWee, Gary, and Marsha. Diversity of combined ipsilateral limb use was highest for Pumpkin, Jake, and Fancy, but lowest for Marsha, PeeWee, and Shone. Contralateral limb use diversity was highest for Pumpkin, Fancy, and Jake, but lowest for Marsha, Peewee, and Cliff.

Linear regression tests resulted in a wide range of correlation magnitudes between positional classification schemas (see Table 4.2.3.4). Diversity scores under the Pos7 and Pos8 classification schemas were effectively uncorrelated with Pos1 and Pos2. Pos1 and Pos4 diversity scores were not meaningfully correlated, but a moderate correlation was found between Pos3 and Pos4. Pos4 diversity was moderately correlated with Pos6, while Pos6 diversity was strongly correlated with Pos3 and Pos8. Pos5 diversity was only correlated with Pos1 and Pos2. Among the limb use categories, the overall Pos1 and Pos5 diversity scores were strongly correlated with diversity scores calculated from ipsilateral and contralateral limb motifs. A moderate relationship existed between the Pos1 diversity measure and the diversity in the use of any individual limb as well as the diversity of engagement with both legs. The diversity in use of both arms was moderately correlated with Pos3 and Pos6 diversity.

Table 4.2.3.5 shows the R^2 values calculated from linear regression tests between different restrictions of the Pos1 classification schema based on the broad positional modes of posture, locomotion, sit and squat, lie, orthograde stand, and pronograde stand. The overall Pos1

Table 4.2.3.4 Correlation Between All Positional and Limb Use Classification Schemas

	Pos1	Pos2	Pos3	Pos4	Pos5	Pos6	Pos7	Pos8	Any Arm	Any Leg	Any Limb	Ipsilateral Limbs	Contralateral Limbs	Both Arms	Both Legs
Pos1	X														
Pos2	0.842	X													
Pos3	0.403	0.350	X												
Pos4	0.102	0.233	0.428	X											
Pos5	0.672	0.844	0.117	0.154	X										
Pos6	0.227	0.275	0.886	0.571	0.066	X									
Pos7	0.037	0.002	0.598	0.249	0.021	0.517	X								
Pos8	0.000	0.000	0.456	0.477	0.041	0.616	0.743	X							
Any Arm	0.332	0.314	0.372	0.139	0.268	0.338	0.126	0.117	X						
Any Leg	0.378	0.304	0.039	0.002	0.428	0.001	0.042	0.233	0.094	X					
Any Limb	0.536	0.460	0.190	0.021	0.541	0.062	0.000	0.042	0.470	0.815	X				
Ipsilateral Limbs	0.765	0.654	0.148	0.002	0.671	0.033	0.011	0.122	0.286	0.733	0.800	X			
Contralateral Limbs	0.783	0.726	0.176	0.017	0.742	0.066	0.009	0.074	0.412	0.686	0.851	0.945	X		
Both Arms	0.346	0.341	0.497	0.085	0.173	0.449	0.127	0.124	0.685	0.090	0.367	0.307	0.397	X	
Both Legs	0.457	0.439	0.007	0.007	0.589	0.011	0.157	0.349	0.098	0.870	0.726	0.792	0.785	0.095	X

Cells contain linear regression R^2 values.
More intense red shading corresponds with higher R^2 values.

Table 4.2.3.5 Pos1 Positional Diversity Correlation Between Different Positional Modes

	Total	Postures	Locomotion	Sit and Squat	Lie	Orthograde Stand	Pronograde Stand
Total	X						
Postures	0.866	X					
Locomotion	0.003	0.052	X				
Sit and Squat	0.227	0.399	0.002	X			
Lie	0.496	0.430	0.085	0.007	X		
Orthograde Stand	0.025	0.018	0.238	0.246	0.011	X	
Pronograde Stand	0.098	0.103	0.018	0.143	0.001	0.001	X

Cells contain linear regression R^2 values.
More intense red shading corresponds with higher R^2 values.

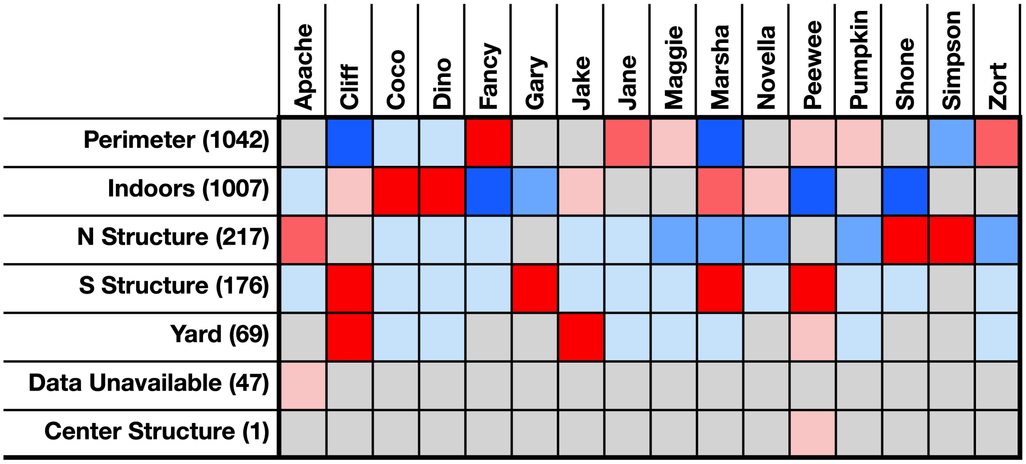
diversity scores were strongly correlated with the Pos1 diversity of postures. Pos1 diversity while lying was moderately correlated with the overall Pos1 diversity and the Pos1 diversity while engaging in postures. Pos1 diversity in the sitting and squatting category was weakly correlated with the overall Pos1 diversity and the Pos1 diversity in postures. The expressed diversity of orthograde standing postures was weakly correlated with the diversity of locomotor modes and the diversity of postures falling under the sitting and squatting category.

4.3 Hypothesis 3: Substrate Use and Enclosure Zone Occupation

4.3.1 Enclosure Zones and Sunlight Exposure

As predicted in Hypothesis 3, subjects showed individual differences in rates of occupation for different zones of their enclosure ($p < 2.2 \text{ x} 10^{-16}$; see Figure 4.3.1.1) that varied from the overall rates of occupation for the entire group (see Figure 4.3.1.2). Marsha and Cliff were the least likely to occupy the perimeter of the outdoor enclosure, whereas Fancy, Sort, and Jane were the most likely to occupy the perimeter ($p < 0.05$). Coco and Dino spent disproportionately large amounts of time indoors, while Fancy, Shone, and PeeWee were the least likely to occupy indoor spaces ($p < 0.05$). Shone and Simpson occupied the north platform structure most frequently, while Cliff, Gary, Marsha, and PeeWee occupied the south platform structure most often ($p < 0.05$). Cliff and Jake were the individuals most likely to be found in the yard during scans ($p < 0.05$). Distinct enclosure zone occupation tendencies among individuals are maintained when zone segregation includes the use of different platforms on the two platform structures ($p < 2.2 \times 10^{-16}$; see Figure S4.3.1.1). Shone, Simpson, and Apache spent disproportionate amounts of time on N1 Front and the lower ramp of the north platform structure ($p < 0.05$). Cliff and PeeWee were the chimpanzees most likely to occupy S1 Front, while Gary and PeeWee were the most likely to occupy the ramp leading to the north platform structure ($p < 0.05$). Marsha occupied S2 Front far more often than any other chimpanzee ($p < 0.05$). Apache was the most likely to reside under the north platform structure and Shone spent a disproportionately high amount of time on S2 Back ($p < 0.05$).

Occupation of different enclosure zones differed between the male and female chimpanzees ($p < 2.2 \times 10^{-16}$; see Table 4.3.1.1). Female chimpanzees spent the plurality of their



	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort
Perimeter (1042)	⬜	🟦	🩵	🩵	🟥	⬜	⬜	🔴	🩷	🟦	⬜	🩷	🩷	⬜	🔵	🔴
Indoors (1007)	🩵	🩷	🟥	🟥	🟦	🔵	🩷	⬜	⬜	🔴	🩷	🟦	⬜	🟦	⬜	⬜
N Structure (217)	🔴	⬜	🩵	🩵	🩵	⬜	🩵	🩵	🔵	🔵	🔵	⬜	🔵	🟥	🟥	🔵
S Structure (176)	🩵	🟥	🩵	🩵	🩵	🟥	🩵	🩵	🩵	🟥	🩵	🟥	🩵	🩵	⬜	🩵
Yard (69)	⬜	🟥	🩵	🩵	⬜	⬜	🟥	🩵	🩵	🩵	⬜	🩷	🩵	⬜	⬜	🩵
Data Unavailable (47)	🩷	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
Center Structure (1)	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🩷	⬜	⬜	⬜	⬜

Figure 4.3.1.1 Overall occupation of enclosure zones were significantly different between subjects (Chi-square = 1560.3, df = 90, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

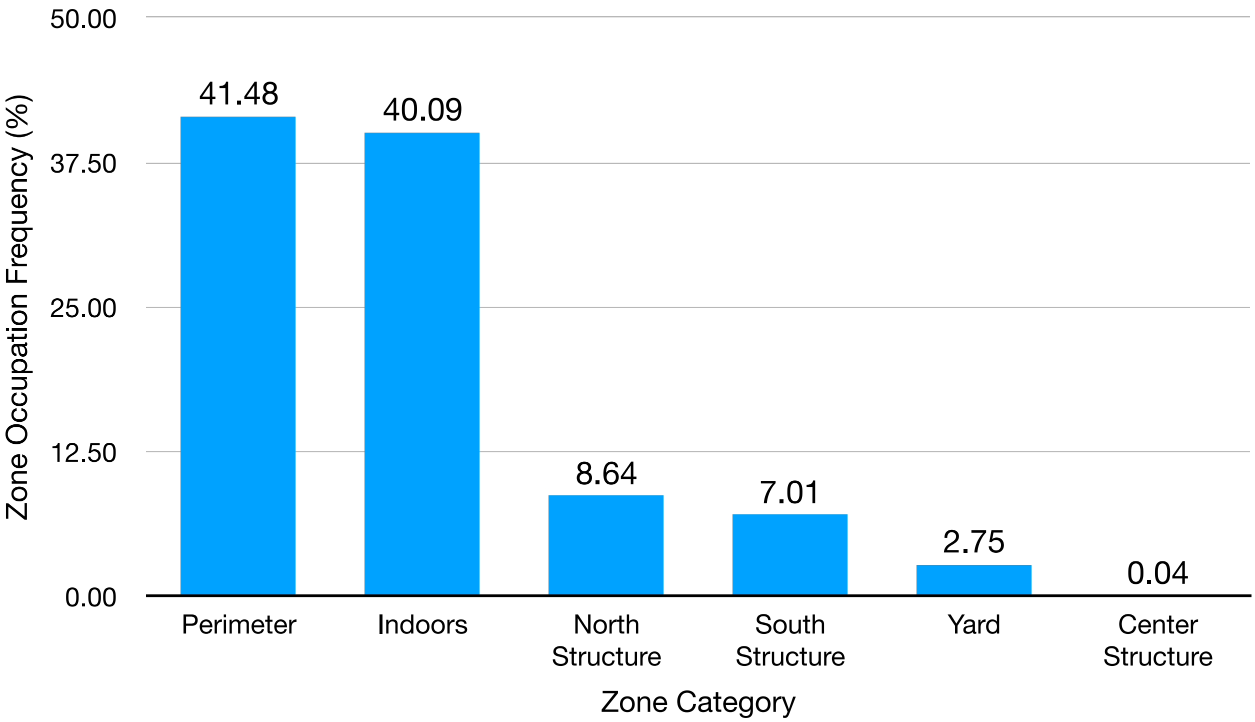


Figure 4.3.1.2 Bars and percentages represent the frequency at which the study group occupied the different zones of their enclosure.

time around the perimeter of the outdoor portion of their enclosure (48.5%) and were more likely than males to occupy the perimeter ($p < 0.05$). In the aggregate, male chimpanzees were more likely to occupy the north end platform structure and the yard of their outdoor enclosure ($p < 0.05$). When considering the differential occupation of different platform levels, females more frequently occupied S2 Front than males, while males more frequently occupied N1 Front, S1 Front, N1 back, the north platform structure's lower ramp, the south platform structure's lower ramp and the area under the south platform structure ($p < 0.05$; see Table S4.3.1.1).

The study group showed different tendencies for enclosure use when comparing between the periods before and after the installation of the climbing aid ($p = 2.315 \times 10^{-15}$; see Table S4.3.1.2). After the group's return to their typical enclosure, they were found more frequently around the perimeter and in the indoor portions of their enclosure, and they spent less time occupying the yard ($p < 0.05$). Focal subject data revealed that S1 Front, N1 Back, N Under

Table 4.3.1.1 Basic Enclosure Zone Occupation Differences by Sex

	Male	Female	Total	% Total	% Male	% Female
Perimeter	-6.06 (587)	6.06 (455)	1042	40.7	36.2	48.5
Indoors	-1.72 (617)	1.72 (390)	1007	39.4	38.1	41.5
N Structure	10.69 (210)	-10.69 (7)	217	8.5	13.0	0.7
S Structure	0.74 (116)	-0.74 (60)	176	6.9	7.2	6.4
Yard	5.40 (65)	-5.40 (4)	69	2.7	4.0	0.4
Data Unavailable	-1.76 (24)	1.76 (23)	47	1.8	1.5	2.4
Center Structure	0.76 (1)	-0.76 (0)	1	0.0	0.1	0.0

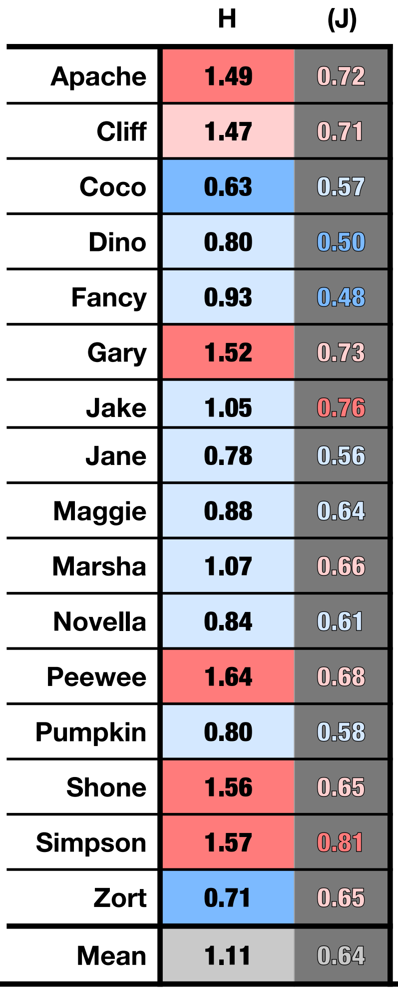
Overall occupation of enclosure zones were significantly different between male and female subjects (Chi-square = 160.72, df = 6, $p < 2.2 \text{ x}10^{-16}$).
See Table 4.2.1.1 for description of cell contents, and shading.

Platform, and N3 were all occupied less often after the group's return to their typical enclosure ($p < 0.05$).

Table 4.3.1.2 displays the calculated Shannon diversity indices for individual occupation rates of enclosure zones. Coco and Zort demonstrate the lowest diversity in their enclosure use, while PeeWee, Simpson, Shone, and Apache demonstrate the highest relative diversity. Simpson and Jake have the most even distributions of enclosure zone occupation rates, while Fancy and Dino have the lowest evenness scores for their enclosure zone use.

Members of this group spent the majority of their time either indoors (43.3%) or in the shade (40.8%) (see Figure 4.3.1.3). Subjects residing in partial shade and in direct sunlight accounted for 8.7% and 7.2% of scans respectively. Individuals showed different rates of experiencing different sunlight exposure categories ($p < 2.2 \text{ x}10^{-16}$; see Figure 4.3.1.4). Jane, Maggie, Marsha, PeeWee and Novella were the most likely to be found in direct sunlight. Shone, PeeWee, Gary, and Apache disproportionately occupied fully shaded spots in their outdoor enclosure ($p < 0.05$). Fancy and Pumpkin were the most likely to occupy partially shaded spots

Table 4.3.1.2 Enclosure Zone Occupation Diversity by Subject



	H	(J)
Apache	1.49	0.72
Cliff	1.47	0.71
Coco	0.63	0.57
Dino	0.80	0.50
Fancy	0.93	0.48
Gary	1.52	0.73
Jake	1.05	0.76
Jane	0.78	0.56
Maggie	0.88	0.64
Marsha	1.07	0.66
Novella	0.84	0.61
Peewee	1.64	0.68
Pumpkin	0.80	0.58
Shone	1.56	0.65
Simpson	1.57	0.81
Zort	0.71	0.65
Mean	1.11	0.64

Shannon diversity index (H) and species evenness (J) calculated from individual rates of occupation for designated zones of their enclosure.
See Table 4.2.3.1 for description of cell shading and text coloring.

in their outdoor enclosure ($p < 0.05$). Tendencies for inhabiting different categories of sunlight exposure differed between male and female chimpanzees ($p < 2.2 \times 10^{-16}$; see Table 4.3.1.3). Throughout the study, males tended to inhabit shaded areas of the enclosure when outdoors to a far greater degree than did the female members of the group ($p < 0.05$). Females were much more likely than males to be found in direct sunlight ($p < 0.05$). Females were also significantly more likely to inhabit spots in their enclosure where they experienced partial sunlight ($p < 0.05$). While profiles of inhabiting different sunlight categories was significantly different between the

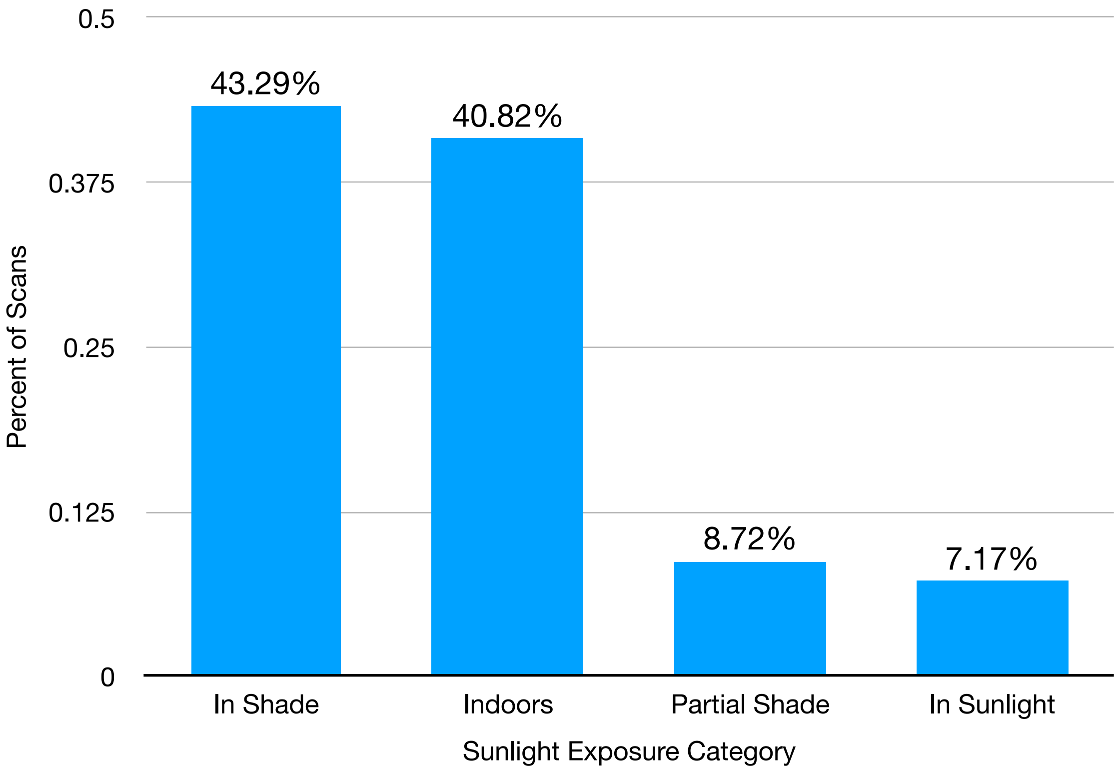


Figure 4.3.1.3 Bars and percentages represent the frequency at which the study group experienced different levels of sunlight exposure.

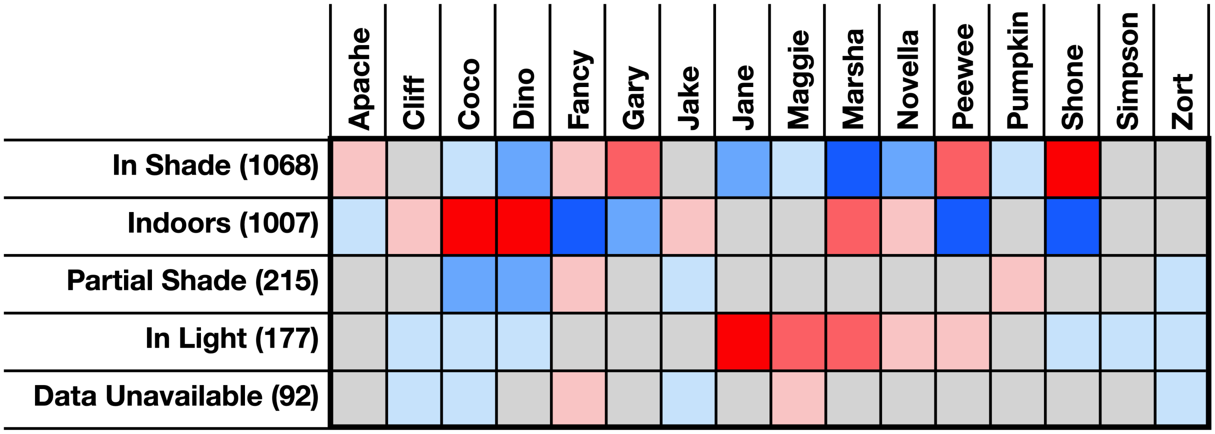


Figure 4.3.1.4 Overall rates of inhabiting different categories of sunlight exposure were significantly different between subjects (Chi-square = 656.18, df = 60, $p < 2.2 \text{ x}10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

periods before and after the climbing aid's installation ($p = 5.961 \text{ x}10^{-6}$; see Table S4.3.1.3), only the rate at which the chimpanzees occupied the indoor portion of their enclosure increased after their return to their typical enclosure, as stated previously ($p < 0.05$).

Table 4.3.1.3 Sunlight Exposure Differences by Sex

	Male	Female	Total	% Total	% Male	% Female
In Shade	9.39 (789)	-9.39 (279)	1068	41.7	48.7	29.7
Indoors	-1.72 (617)	1.72 (390)	1007	39.4	38.1	41.5
Partial Shade	-3.27 (114)	3.27 (101)	215	8.4	7.0	10.8
In Light	-9.22 (55)	9.22 (122)	177	6.9	3.4	13.0
Data Unavailable	-2.92 (45)	2.92 (47)	92	3.6	2.8	5.0

Overall rates of inhabiting different categories of sunlight exposure were significantly different between male and female subjects (Chi-square = 150.32, df = 4, $p < 2.2 \times 10^{-16}$).
See Table 4.2.1.1 for description of cell contents, and shading.

4.3.2 Substrate Use

In agreement with Hypothesis 3, subjects showed distinct patterns of use for the substrates available to them in their enclosure ($p < 2.2 \times 10^{-16}$; see Figure 4.3.2.1). The most common substrates with which the chimpanzees engaged were the concrete ground, metal mesh, metal shelf, concrete wall, and food ($p < 0.05$). Pumpkin was the individual least likely to occupy the concrete ground, while Zort was the most likely to be found on the concrete ground ($p < 0.05$). The metal mesh was most commonly used by Maggie, Jane, Novella, and Pumpkin, and was used least often by Coco and Cliff ($p < 0.05$). Metal shelves were most often used by Novella, Pumpkin, Maggie, Jane, and Fancy, and were occupied rarely or never by Cliff, Gary, Jake, Marsha, Simpson, and Zort ($p < 0.05$). Coco and Dino were observed in association with concrete walls most frequently, while Maggie and Novella were the least likely to be observed engaging with concrete walls ($p < 0.05$). Similar patterns of individual substrate use were present when substrates were sorted by their morphological characteristics ($p < 2.2 \times 10^{-16}$; see Figure S4.3.2.1).

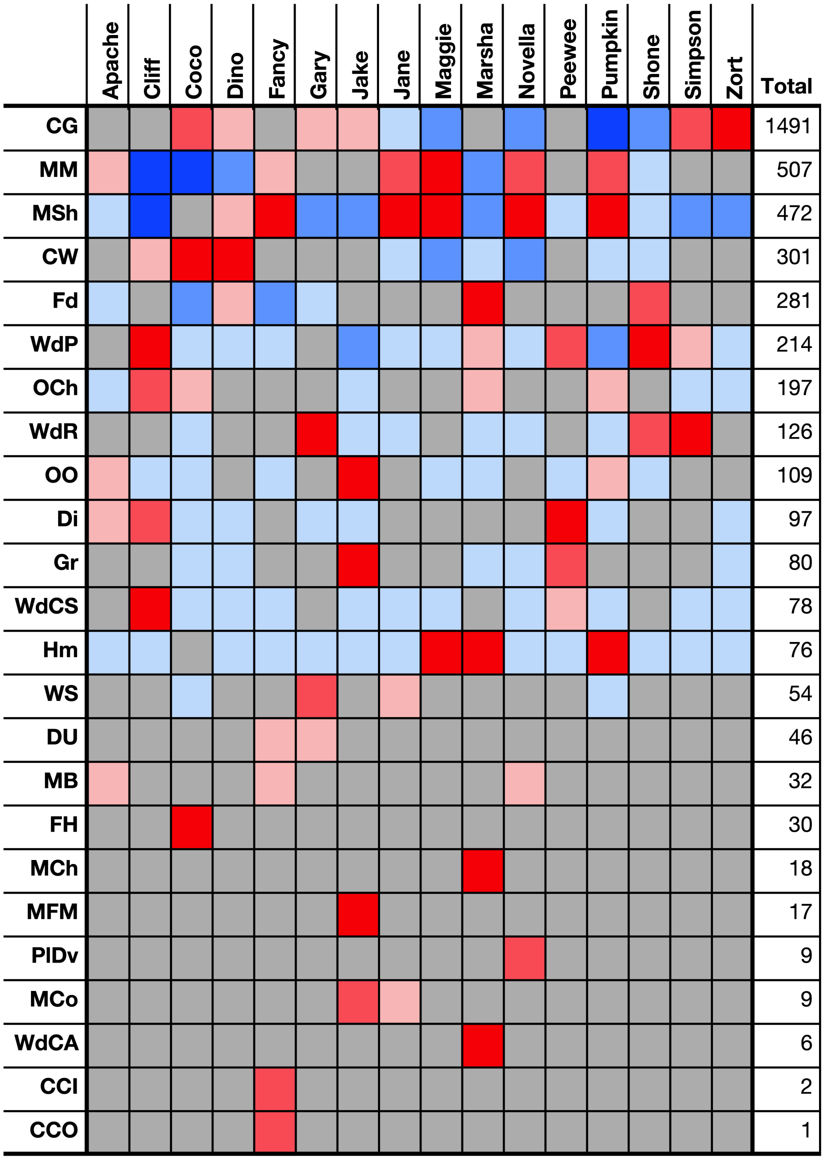


Figure 4.3.2.1 The differing tendencies for individuals to associate with each available substrate in their enclosure (Chi-square = 4086.1, df = 345, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

Substrate use was significantly different between male and female subjects ($p < 2.2 \times 10^{-16}$; see Table 4.3.2.1). The males in the group tended to associate with the concrete ground, concrete walls, wooden platforms, wooden ramps, and wooden columns, while female group members were most likely to associate with metal mesh, metal shelves, hammocks, and metal chains ($p < 0.05$).

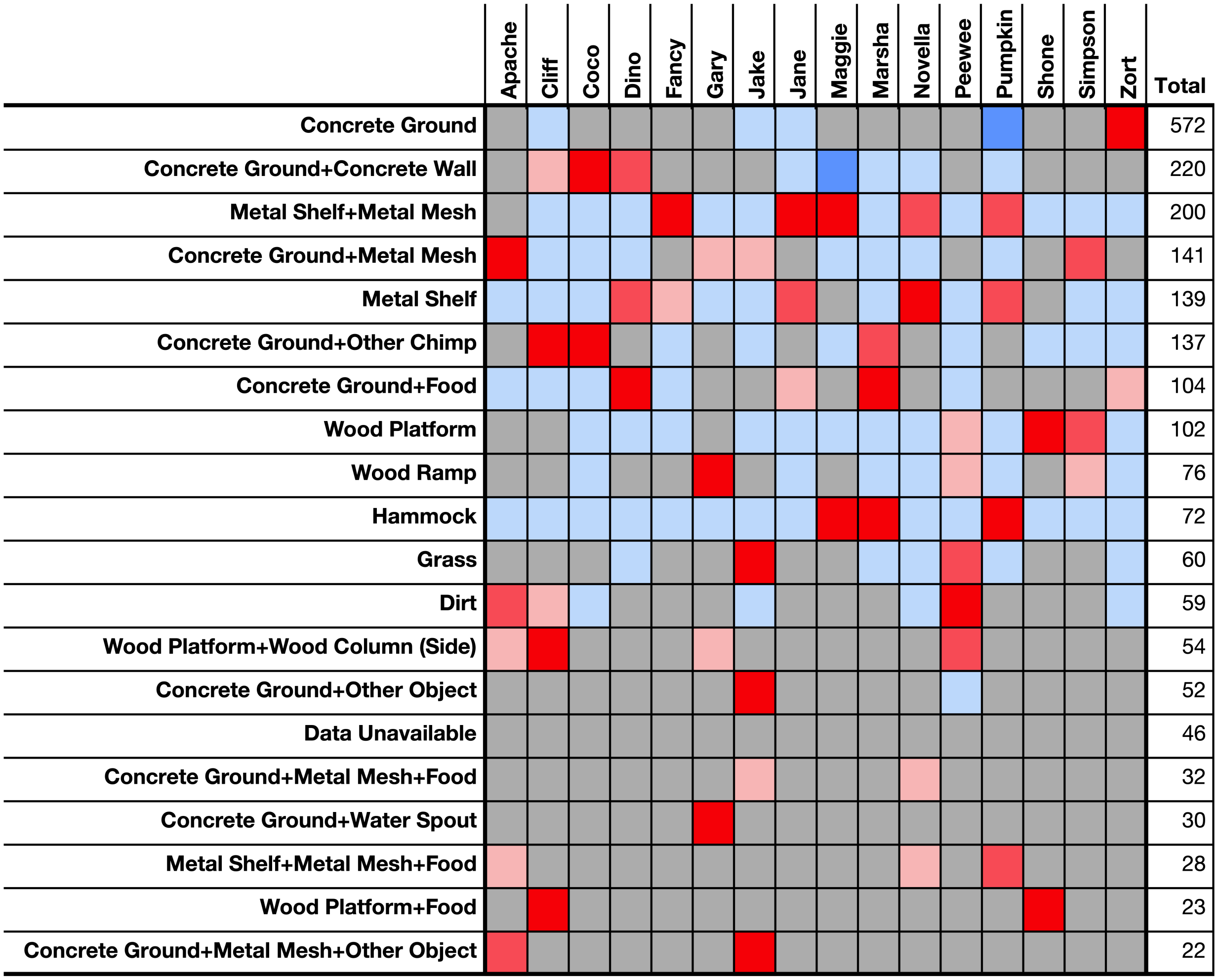
Table 4.3.2.1 Substrate Affiliation Differences by Sex

	Male	Female	Total	% Total	% Male	% Female
CG	10.518 (1082)	-10.518 (409)	1491	35.06	41.09	25.25
MM	-9.733 (214)	9.733 (293)	507	11.92	8.13	18.09
MSh	-18.116 (112)	18.116 (360)	472	11.10	4.25	22.22
CW	8.207 (253)	-8.207 (48)	301	7.08	9.61	2.96
Fd	-3.428 (147)	3.428 (134)	281	6.61	5.58	8.27
WdP	8.452 (191)	-8.452 (23)	214	5.03	7.25	1.42
OCh	-2.548 (105)	2.548 (92)	197	4.63	3.99	5.68
WdR	7.076 (116)	-7.076 (10)	126	2.96	4.41	0.62
OO	2.102 (78)	-2.102 (31)	109	2.56	2.96	1.91
Di	2.527 (72)	-2.527 (25)	97	2.28	2.73	1.54
Gr	3.596 (65)	-3.596 (15)	80	1.88	2.47	0.93
WdCS	5.345 (71)	-5.345 (7)	78	1.83	2.70	0.43
Hm	-10.976 (1)	10.976 (75)	76	1.79	0.04	4.63
WS	1.007 (37)	-1.007 (17)	54	1.27	1.41	1.05
DU	-1.672 (23)	1.672 (23)	46	1.08	0.87	1.42
MB	-2.489 (13)	2.489 (19)	32	0.75	0.49	1.17
FH	3.180 (27)	-3.180 (3)	30	0.71	1.03	0.19
MCh	-5.420 (0)	5.420 (18)	18	0.42	0.00	1.11
MFM	2.240 (15)	-2.240 (2)	17	0.40	0.57	0.12
PlDv	-0.393 (5)	0.393 (4)	9	0.21	0.19	0.25
MCo	-0.393 (5)	0.393 (4)	9	0.21	0.19	0.25
WdCA	-2.284 (1)	2.284 (5)	6	0.14	0.04	0.31
CCl	-1.803 (0)	1.803 (2)	2	0.05	0.00	0.12
CCO	-1.275 (0)	1.275 (1)	1	0.02	0.00	0.06

The overall rates of associating with particular substrates were significantly different between male and female subjects (Chi-square = 877.44, df = 23, p < 2.2 x10^{-16}).
See Table 4.2.1.1 for description of cell contents, and shading.

Tendencies for chimpanzees to associate with combinations of substrates also varied depending on the individual (p < 2.2 x10^{-16}; see Figure 4.3.2.2). The most frequently used combinations of substrates involved either concrete ground or metal mesh ($p < 0.05$). Use of the metal shelves and metal mesh was more characteristic of Maggie, Jane, Fancy, Novella and Pumpkin, whereas use of the concrete ground and metal mesh was most characteristic of Apache, Simpson, Gary, and Jake ($p < 0.05$).

Substrate use tendencies were different before versus after the installation of the climbing aid ($p < 2.2 \times 10^{-16}$; see Table 4.3.2.2). Decreases were observed in the chimpanzees' engagement with the sides of the wood columns, dirt ground, wooden platforms, and metal chain ($p < 0.05$).



	Total
Concrete Ground	572
Concrete Ground+Concrete Wall	220
Metal Shelf+Metal Mesh	200
Concrete Ground+Metal Mesh	141
Metal Shelf	139
Concrete Ground+Other Chimp	137
Concrete Ground+Food	104
Wood Platform	102
Wood Ramp	76
Hammock	72
Grass	60
Dirt	59
Wood Platform+Wood Column (Side)	54
Concrete Ground+Other Object	52
Data Unavailable	46
Concrete Ground+Metal Mesh+Food	32
Concrete Ground+Water Spout	30
Metal Shelf+Metal Mesh+Food	28
Wood Platform+Food	23
Concrete Ground+Metal Mesh+Other Object	22

Figure 4.3.2.2 The differing tendencies for individuals to associate with combinations of available substrates in their enclosure (Chi-square = 7104.5, df = 1635, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

Table 4.3.2.2 Substrate Affiliation Differences by Study Period

	Before	After	Total	% Total	% Before	% After
CG	-4.140 (676)	4.140 (815)	1491	34.69	32.01	37.28
MM	-2.439 (226)	2.439 (281)	507	11.80	10.70	12.85
MSh	1.231 (247)	-1.231 (225)	472	10.98	11.70	10.29
CW	2.933 (174)	-2.933 (127)	301	7.00	8.24	5.81
Fd	-1.178 (130)	1.178 (151)	281	6.54	6.16	6.91
WdP	4.452 (138)	-4.452 (76)	214	4.98	6.53	3.48
OCh	-4.061 (70)	4.061 (127)	197	4.58	3.31	5.81
WdR	-1.188 (56)	1.188 (70)	126	2.93	2.65	3.20
OO	-4.489 (31)	4.489 (78)	109	2.54	1.47	3.57
Di	5.306 (74)	-5.306 (23)	97	2.26	3.50	1.05
DU	5.383 (41)	-5.383 (5)	91	2.12	1.94	2.29
Gr	1.868 (48)	-1.868 (32)	80	1.86	2.27	1.46
WdCS	7.832 (73)	-7.832 (5)	78	1.81	3.46	0.23
Hm	-2.487 (27)	2.487 (49)	76	1.77	1.28	2.24
WS	0.872 (30)	-0.872 (24)	54	1.26	1.42	1.10
MB	0.039 (16)	-0.039 (16)	32	0.74	0.76	0.73
FH	-1.795 (10)	1.795 (20)	30	0.70	0.47	0.91
MCh	4.281 (18)	-4.281 (0)	18	0.42	0.85	0.00
MFM	3.674 (16)	-3.674 (1)	17	0.40	0.76	0.05
PlDv	-0.981 (3)	0.981 (6)	9	0.21	0.14	0.27
MCo	0.354 (5)	-0.354 (4)	9	0.21	0.24	0.18
WdCA	-2.435 (0)	2.435 (6)	6	0.14	0.00	0.27
CCl	1.424 (2)	-1.424 (0)	2	0.05	0.09	0.00
CCO	1.007 (1)	-1.007 (0)	1	0.02	0.05	0.00

The overall tendencies for the chimpanzees to associate with each available substrate in their enclosure differed significantly between the periods before and after the installation of the climbing aid (Chi-square = 254.13, df = 23, $p < 2.2 \text{ x}10^{-16}$).
See Table 4.2.1.1 for description of cell contents, and shading.

The group increased their engagement with the concrete ground, other conspecifics, and other manipulable objects ($p < 0.05$). Weaker but significant increases in substrate use were observed for metal mesh, hammocks, and the climbing aid, which was notably used by two individuals during six focal scans ($p < 0.05$).

The diversity of each subject's tendency to associate with different substrates and substrate combinations is represented in Table 4.3.2.3. Zort and Coco demonstrated the lowest values for substrate use and substrate combination use diversity. Pumpkin and Apache

Table 4.3.2.3 Substrate Use Diversity by Subject

	Substrates		Substrate Combinations	
	H	*(J)*	H	*(J)*
Apache	**2.18**	0.79	**2.76**	*0.85*
Cliff	**2.04**	0.75	**2.44**	*0.79*
Coco	**1.51**	0.63	**1.90**	*0.69*
Dino	**1.67**	0.67	**2.15**	*0.76*
Fancy	**1.90**	0.72	**2.29**	*0.77*
Gary	**2.01**	0.76	**2.55**	*0.81*
Jake	**1.78**	0.72	**2.50**	*0.85*
Jane	**1.94**	0.73	**2.61**	*0.79*
Maggie	**1.98**	0.75	**2.34**	*0.71*
Marsha	**2.11**	0.75	**2.46**	*0.78*
Novella	**1.75**	0.71	**2.20**	*0.71*
Peewee	**2.18**	0.85	**2.69**	*0.82*
Pumpkin	**2.04**	0.82	**2.82**	*0.81*
Shone	**2.10**	0.80	**2.56**	*0.81*
Simpson	**1.77**	0.71	**2.30**	*0.80*
Zort	**1.12**	0.51	**1.41**	*0.57*
Mean	**1.88**	0.73	**2.37**	0.77

Shannon diversity index (H) and species evenness (J) calculated for each individual based on their rates of use for particular substrates and substrate combinations.
See Table 4.2.3.1 for description of cell shading and text coloring.

demonstrated the highest diversity of substrate combination use, while Apache and PeeWee were characterized by the highest diversity of individual substrate use.

4.4 Hypothesis 4: Substrate and Positional Behavior Associations

4.4.1 Substrate Positional Profiles

As predicted by Hypothesis 4 positional mode occurrence frequencies were varied depending on the substrate with which the focal subject engaged (under Pos7, $p < 2.2 \times 10^{-16}$; see Table 4.4.1.1). Use of the side of the wooden columns, wooden platforms, concrete wall, and metal flex-mesh disproportionately cooccurred with subjects sitting on their buttocks ($p < 0.05$). Squatting was performed most often when the subject was engaging with the metal mesh ($p < 0.05$). Side squatting was similarly associated with the metal mesh, but also with food ($p < 0.05$). Metal shelves, other objects, fire hoses, hammocks, and wooden platforms were associated with lying on one's side ($p < 0.05$). Lying on one's back occurred with the highest likelihood when an individual associated with wooden ramps and concrete walls ($p < 0.05$). Pronograde quadrupedal walking occurred most often on the concrete, grass, and dirt ground ($p < 0.05$). Group members stood in a pronograde orientation most often when in contact with waterspouts, food, and concrete ground ($p < 0.05$).

Examining substrate use by Pos4 positional category reveals additional insights ($p < 2.2 \times 10^{-16}$; see Figure 4.4.1.2). Lateral Lie occurred very seldom on the concrete ground, and Chair-Sit was rarely on the metal shelves ($p < 0.05$). Sit-Out was observed most commonly in association with food, conspecifics, wooden platforms, and wooden ramps ($p < 0.05$). Sit-in was most prevalent when in contact with the sides of the wood columns. Tripedal stand was most frequent when in contact with a waterspout ($p < 0.05$).

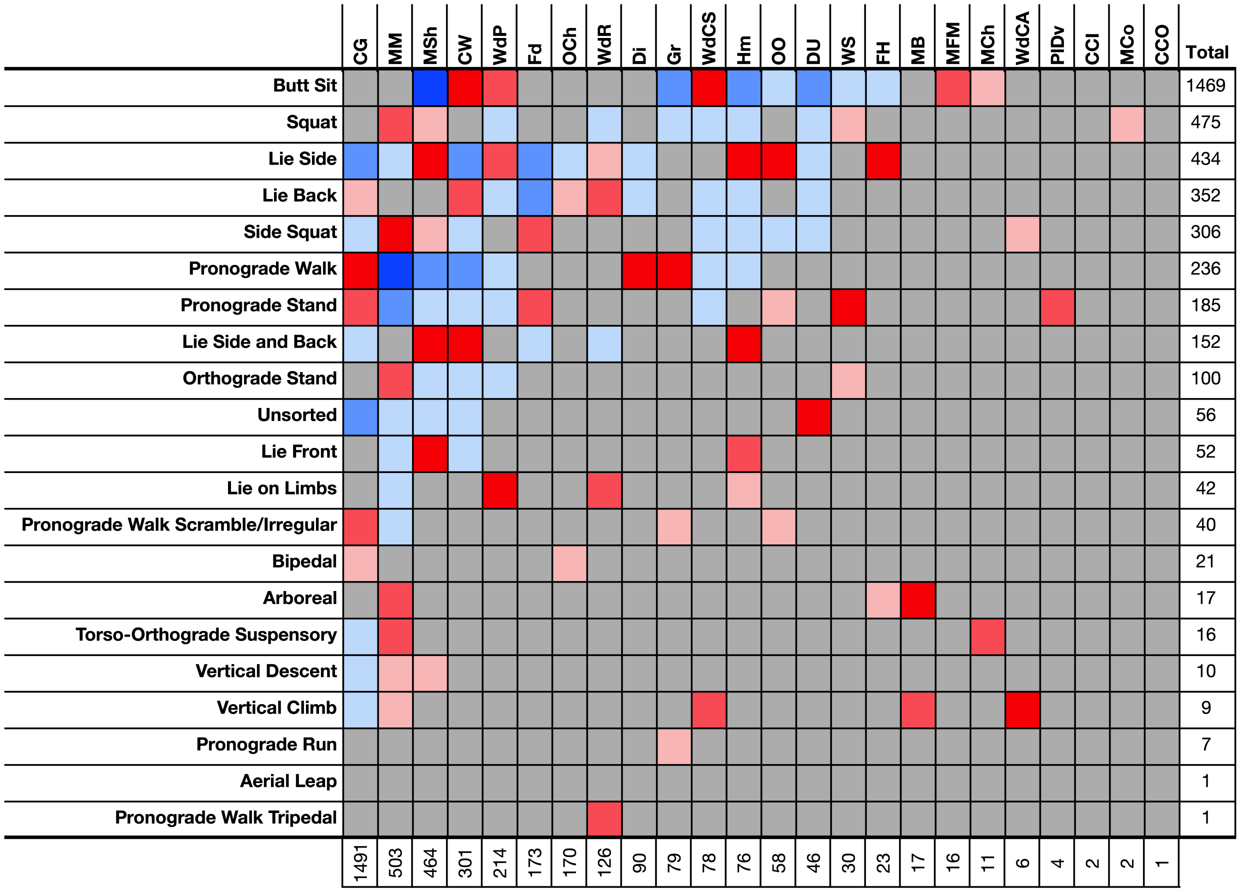


Figure 4.4.1.1 The tendencies for subjects to engage in positional behaviors under the Pos7 classification schema were significantly different when subjects associated with different substrates (Chi-square = 5569.7, df = 460, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

Positional behavior tendencies also varied by substrate under the Pos3 classification schema ($p < 2.2 \times 10^{-16}$; see Figure S4.4.1.1). Contact with a hammock or fire hose were most likely to result in lying on one's side with their arm out ($p < 0.05$). Sitting on one's buttocks with their arms suspended was most commonly associated with metal chains and metal mesh ($p < 0.05$). Squatting without the support of one's forelimbs occurred most often when interacting with food or a water spout ($p < 0.05$). Squatting while engaging one arm in compression was most common in association with conspecifics ($p < 0.05$).

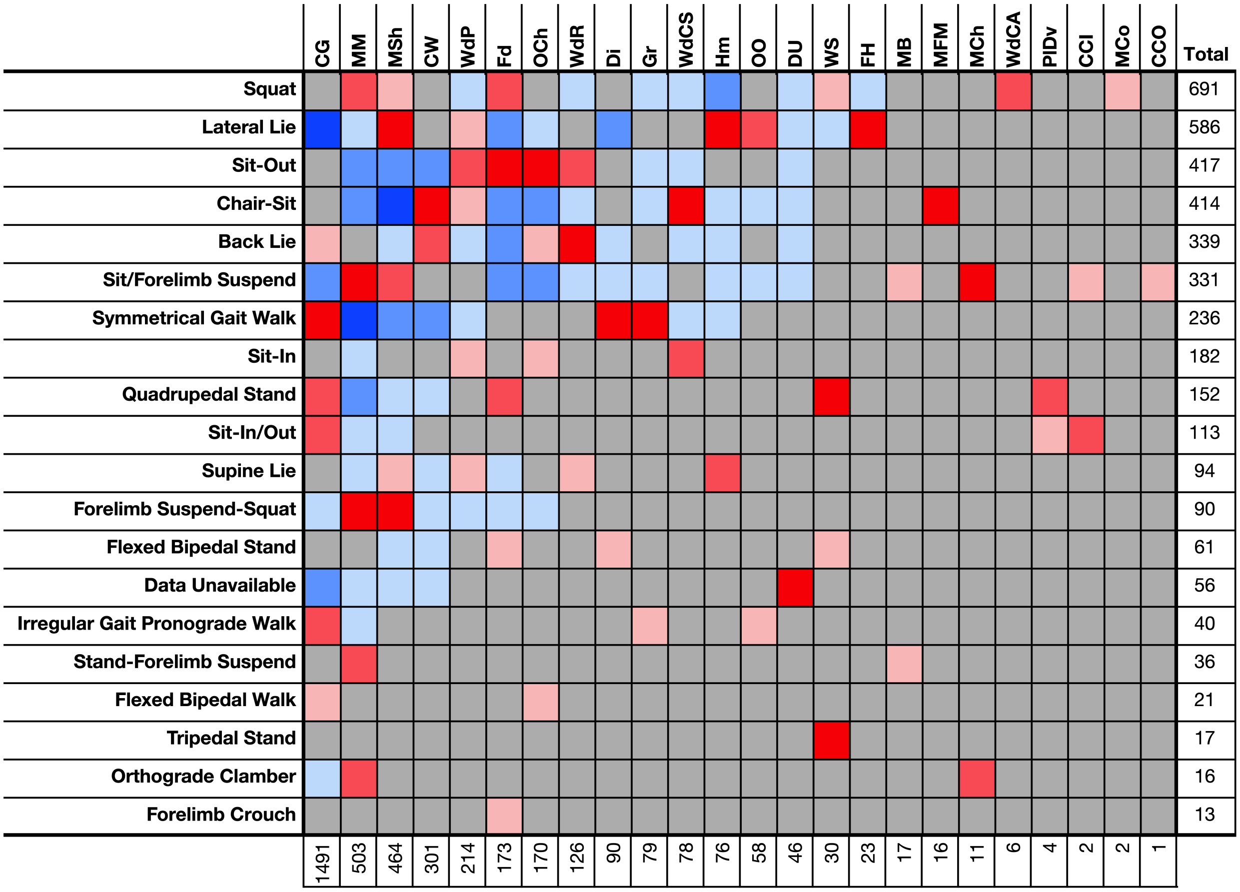
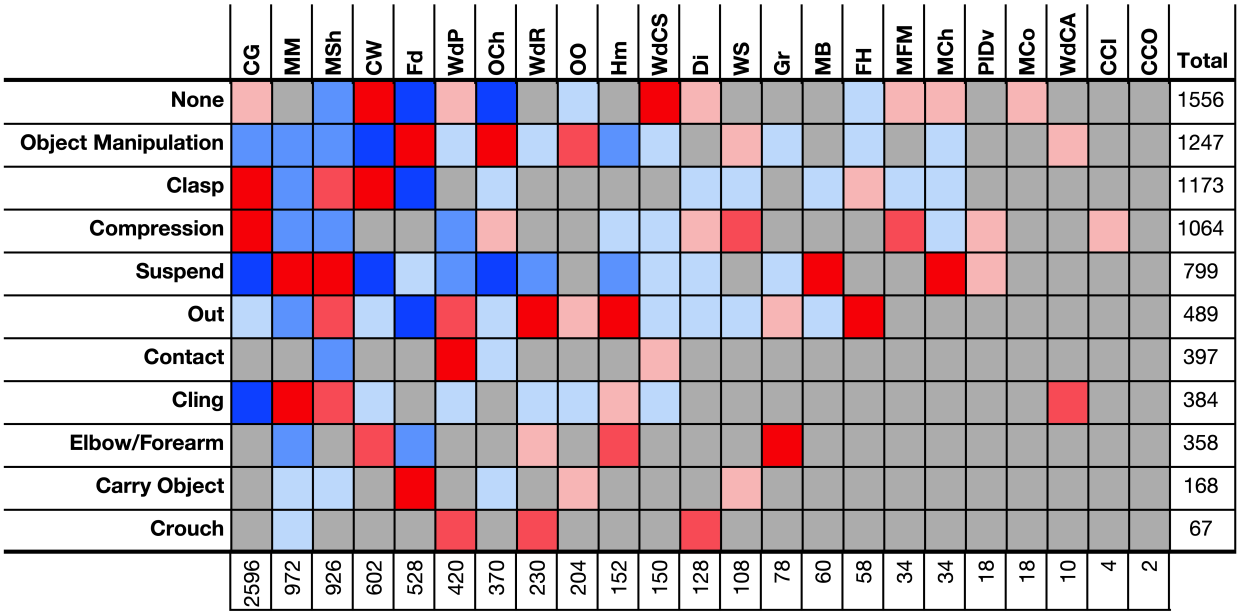


Figure 4.4.1.2 The tendencies for subjects to engage in positional behaviors under the Pos4 classification schema were significantly different when subjects associated with different substrates (Chi-square = 7185.2, df = 736, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

The manner of use of one's forelimbs were significantly different depending on the substrates with which they engaged ($p < 2.2 \times 10^{-16}$; see Table 4.4.1.3). Lack of forelimb use occurred most often in association with concrete walls and the sides of the wooden columns ($p < 0.05$). Group members clasped their arms on their own body most frequently on the concrete ground and in association with concrete walls ($p < 0.05$). Object manipulation occurred most often in association with food, conspecifics, and other objects ($p < 0.05$). Arm suspension was employed most likely when a subject interacted with metal mesh, metal bars, metal shelves, and



	CG	MM	MSh	CW	Fd	WdP	OCh	WdR	OO	Hm	WdCS	Di	WS	Gr	MB	FH	MFM	MCh	PlDv	MCo	WdCA	CCl	CCO	Total
None																								1556
Object Manipulation																								1247
Clasp																								1173
Compression																								1064
Suspend																								799
Out																								489
Contact																								397
Cling																								384
Elbow/Forearm																								358
Carry Object																								168
Crouch																								67
	2596	972	926	602	528	420	370	230	204	152	150	128	108	78	60	58	34	34	18	18	10	4	2	

Figure 4.4.1.3 The tendencies for subjects to engage modes of forelimb use were significantly different when subjects associated with different substrates (Chi-square = 3454.1, df = 220, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

metal chains ($p < 0.05$). Rates of arm clinging were highest with the use of metal mesh, metal shelves, and the climbing aid ($p < 0.05$).

Patterns of hindlimb use were also dependent on substrates used ($p < 2.2 \times 10^{-16}$; see Table 4.4.1.4). Bent-compression was most strongly linked to food, metal mesh, and the climbing aid, and was least likely to occur in association with hammocks, fire hoses, wooden ramps, concrete ground, and other objects ($p < 0.05$). Legs were observed in their mid-compression state with the greatest likelihood in association with concrete walls, the concrete ground, dirt, wood ramps, and food ($p < 0.05$). Legs were extended out at the highest rate in association with wooden platforms, metal shelves, fire hoses, hammocks, and metal chains ($p < 0.05$). Legs were "In" most often in association with hammocks, metal shelves, and metal FlexMesh ($p < 0.05$).

4.4.2 Substrate Positional Diversity

Positional diversity as calculated according to the associated substrate used by the focal subject under Pos1, Pos3, and Pos4 are displayed in Table 4.4.2.1. Positional diversity by substrate combination is portrayed in Table S4.4.2.1. The highest positional diversity scores were associated with the concrete ground, metal mesh, and metal shelves under Pos1 and Pos3. Positional diversity was highest under Pos4 for the concrete ground, metal mesh, and conspecific contact. Positional diversity scores tended to be lower for use of the concrete culverts, metal chains, metal columns, metal FlexMesh, plastic dividers, and the climbing aid. Positional diversity was highest for the combined substrate use of metal shelf and metal mesh, concrete ground and metal mesh, and concrete ground and concrete wall.

Diversity of engagement for any given arm or leg is displayed in Table 4.4.2.2. Arm use was most diverse when a chimpanzee was associated with metal shelves, other objects, wooden

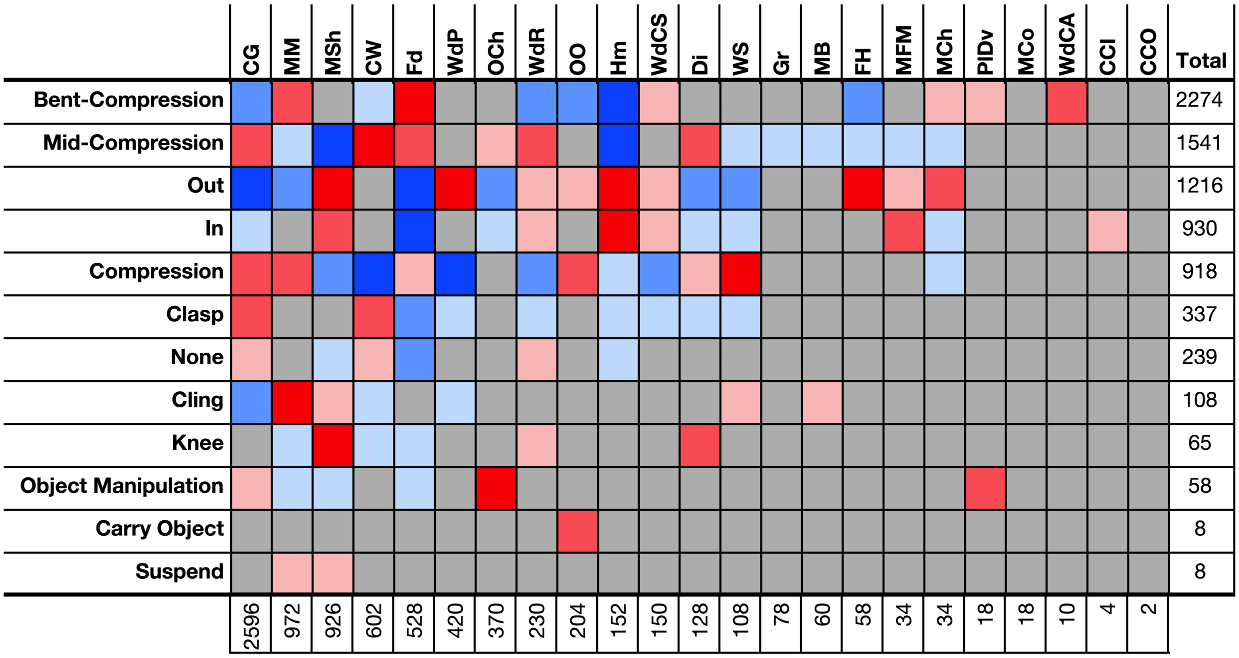


Figure 4.4.1.4 The tendencies for subjects to engage modes of hindlimb use were significantly different when subjects associated with different substrates (Chi-square = 2332.6, df = 242, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

Table 4.4.2.1 Positional Diversity by Substrate

	Pos1		Pos3		Pos4	
	H	J	H	J	H	J
CCl	0.69	1.00	0.69	1.00	0.69	1.00
CCO	0.00	NA	0.00	NA	0.00	NA
CG	4.85	0.83	3.24	0.71	2.60	0.80
CW	3.89	0.85	2.34	0.73	1.70	0.77
Di	2.68	0.79	2.11	0.73	1.97	0.79
DU	0.10	0.15	0.10	0.15	0.10	0.15
Fd	3.84	0.89	2.54	0.73	1.82	0.67
FH	1.77	0.71	1.17	0.65	0.64	0.46
Gr	2.31	0.72	2.03	0.72	1.80	0.70
Hm	3.19	0.90	2.30	0.78	1.02	0.46
MB	3.10	0.96	2.64	0.91	1.73	0.83
MCh	1.01	0.73	0.43	0.39	0.30	0.44
MCo	1.43	0.89	1.43	0.89	0.00	NA
MFM	1.65	0.85	0.87	0.54	0.46	0.42
MM	5.02	0.93	3.61	0.82	2.33	0.73
MSh	4.84	0.91	3.64	0.84	2.06	0.68
OCh	3.83	0.87	2.79	0.77	2.14	0.77
OO	3.71	0.94	2.85	0.86	1.95	0.81
PlDv	1.68	0.94	1.68	0.94	1.04	0.95
WdCA	1.33	0.96	0.87	0.79	0.45	0.65
WdCS	2.76	0.88	1.58	0.63	1.40	0.64
WdP	3.71	0.88	2.51	0.73	2.12	0.83
WdR	3.58	0.91	2.62	0.86	2.04	0.82
WS	2.86	0.90	2.53	0.84	1.48	0.83
Mean	2.88	0.89	2.15	0.77	1.40	0.70

Shannon diversity index (H) and species evenness (J) calculated for each substrate based on their associated rates of positional behavior categories under the Pos1, Pos3, and Pos4 classification schemas.
See Table 4.2.3.1 for description of cell shading and text coloring.

Table 4.4.2.2 Diversity of Forelimb and Hindlimb Use by Substrate

	Any Arm			Any Leg	
	H	J		H	J
OO	*2.12*	0.88	**OO**	*1.91*	0.87
MSh	*2.12*	0.88	**CG**	*1.90*	0.76
WdP	*2.11*	0.88	**OCh**	*1.87*	0.78
CG	*2.07*	0.87	**MSh**	*1.83*	0.76
Gr	*2.05*	0.89	**MM**	*1.81*	0.75
WdR	*2.00*	0.91	**MB**	*1.78*	0.86
MM	*1.97*	0.82	**CW**	*1.76*	0.85
CW	*1.92*	0.80	**Gr**	*1.69*	0.81
Di	*1.88*	0.82	**WdR**	*1.67*	0.86
Hm	*1.83*	0.83	**WdP**	*1.51*	0.69
WS	*1.76*	0.80	**Di**	*1.49*	0.72
Fd	*1.69*	0.70	**WdCS**	*1.45*	0.75
MB	*1.66*	0.85	**Fd**	*1.35*	0.65
FH	*1.59*	0.89	**PlDv**	*1.27*	0.79
WdCS	*1.56*	0.68	**MFM**	*1.27*	0.79
OCh	*1.53*	0.67	**MCo**	*1.22*	0.88
PlDv	*1.44*	0.89	**WS**	*1.18*	0.66
MCo	*1.37*	0.85	**FH**	*1.10*	0.61
MFM	*1.21*	0.75	**CCl**	*1.04*	0.95
WdCA	*1.19*	0.86	**Hm**	*0.92*	0.66
MCh	*0.99*	0.71	**CCO**	*0.69*	1.00
CCO	*0.69*	1.00	**MCh**	*0.69*	1.00
CCl	*0.56*	0.81	**WdCA**	*0.00*	NA
Mean	**1.62**	0.83	**Mean**	**1.36**	0.79

Shannon diversity index (H) and species evenness (J) calculated for each substrate based on their rates of associated arm and leg engagement types.
See Table 4.2.3.1 for description of cell shading and text coloring.

platforms, and the concrete ground, but was lowest for use of the metal chain and concrete culvert. Leg use diversity was highest when associated with the concrete ground, other chimpanzees, and other objects. Leg use diversity was lowest for use of the climbing aid, concrete culvert, and metal chain.

4.5 Overview of Results

Based on the results presented in this chapter, Hypothesis 1 was not supported. The introduction of the novel vertical climbing aid did not increase the frequency of climbing behaviors, rates of platform structure occupation, or rates of elevated platform level occupation. The null hypothesis that the climbing aid was ineffective at increasing rates of climbing and occupation on the platform structure cannot be rejected. The data support Hypothesis 2 that individuals express different positional behaviors at different rates. Enclosure occupation, sunlight exposure, and substrate use data support Hypothesis 3. Individual subjects showed distinct patterns of substrate and enclosure space use. Finally, rates of expression for different positional behaviors and positional elements differed depending on the substrate(s) that the subjects associated with. Thus, the data presented in this thesis provides evidence in support of Hypothesis 4.

Chapter 5: Discussion

5.1 Climbing Aid Assessment

From the data presented in this thesis, I cannot conclude that the climbing aid was effective at meeting its goal of increasing rates of climbing and vertical space use among the chimpanzees in this study group. Not only did the frequency of level changes diminish on the experimental (south) platform structure, but this same trend was not significant on the control (north) platform structure. Furthermore, after the climbing aid was installed, rates of ascent using only wooden supports were significantly reduced on the experimental platform structure, but not on the control platform structure. However, the short duration of this study, low number of trials, small difference in altered use between platform structures, and the existence of several confounding variables prevent me from giving a definitive declaration on the overall impact and potential benefits or costs from future installation of the climbing aid in chimpanzee enclosures.

It may be the case that the group's more limited than expected use of the climbing aid was due to the group as a whole exhibiting some degree of neophobia and negative bias toward the new stimulus. Certain individuals may have been averse to using the climbing aid because of its relatively novel combined morphological and material characteristics. Pressure treated wood was selected as the material for constructing the climbing aid in part because of its similar composition to the wooden columns that constitute the platform structures. However, the subjects were not as familiar with this exact material presented in such a low diameter form. Moreover, the zig-zag shape of the climbing aid may have been a significant enough departure from the shapes of substrates that the subjects were used to utilizing.

The source of aversion to using the novel climbing aid may have been anxiety-driven, as any unfamiliar stimulus could induce fear in an animal based on their lack of knowledge of the potential consequences of interacting with the stimulus (Coleman and Pierre 2014). Individuals may have exhibited anxiety toward the use of the climbing aid because they are uncertain about the potential negative outcomes associated with sustaining contact with it or using it to climb. Furthermore, a change to the enclosure such as the installation of the climbing aid could signify to a chimpanzee that other changes were also made, and the enclosure as a whole may not be as reliably safe or predictable. In this case, individuals would be compelled to avoid use of the novel climbing aid, not only out of fear of negative outcomes associated with its use, but because it would be imperative to investigate the remainder of the enclosure to identify any other notable changes.

Individual chimpanzees can employ distinct strategies to cope with stress (Spijkerman et al. 1994). Captive chimpanzees and gorillas also show individual patterns of enclosure space use (Ross et al. 2011). Given that individuals in this study also showed distinct patterns of use for elements of their enclosures, behaviors involving the use of certain substrates and enclosure areas may be used as a source of comfort and a means of coping with stress. If members of this group were stressed from the introduction of the climbing aid or any other factor present after the group's reintroduction to their typical enclosure, they may have preferred to associate with familiar substrates as part of their overall means of creating predictability in the face of anxiety.

An alternative, or complementary, explanation for the tendency of chimpanzees to refrain from using the new features of their enclosure to their full extent is offered by Duncan et al. (2022). Chimpanzees with limited experience using alternative features to those present in their environment during large portions or key stages of their lives may exhibit a behavioral inertia that reproduces space use tendencies and limits the imaginations of individuals for how they may use other features in their environment. If the climbing aid was seen as different enough from what a particular chimpanzee was familiar with, they may have failed to incorporate it into personal repertoire of usable substrates. Furthermore, regardless of the climbing aid's actual impact on the ease at which subjects could engage in vertical climbing, the sides of the wooden columns that were altered during this study appeared to have a characteristic use apart from vertical climbing. Certain chimpanzees in the study group tended to use the sides of the wooden columns to lean against while sitting (see Figure 4.4.1.2). The tendency for the group to engage in the Chair-Sit behavior was significantly reduced after the group's return to the enclosure (see Table 4.2.1.3). Use of the sides of the wooden columns was also reduced from 3.45% of scans to 0.23% of scans (see Table 4.3.2.2). However, use of the sides of the column on the unaltered north platform structure was completely absent during the second period of the study, and use of the concrete wall was also reduced during this portion of the study (see Table 4.3.2.3). It is therefore hard to say definitively that the climbing aid presented an obstacle for individuals wishing to engage in the posture of sitting while leaning against the wooden column. However, if individuals spent less time around the south platform structure because there were fewer desired spots to rest at its base or among the higher elevation levels, they may have encountered fewer opportunities to climb upon and occupy the experimental platform structure.

The potential for the climbing aid to disrupt the means by which the chimpanzees typically interacted with the platform structure would have also extended to their experience of climbing on the south platform structure. When climbing on the platform structure using the bare columns, the chimpanzees most often slowly ascended to higher elevation levels by first stepping onto any available horizontal metal bar. After this, they would usually grasp onto the wooden column, often while leaning their forearms onto the higher platform, and put one foot on the end of the platform to which they were ascending. They would then shift their weight from the metal bar to the three limbs already in contact with the higher elevation level.

When ascending using the climbing aid, the chimpanzees would have to experience the novel visual, tactile, and olfactory features of the climbing aid. They would also need to grasp the wood at distances wider apart than on a bare wooden column. If occupants of this enclosure developed certain strategies for making their ascent, they may have been unable to perform these in the same manner after the climbing aid was introduced and may have then avoided ascending to a higher platform level altogether if their motivation for climbing was not strong enough. The novelty of the climbing aid and the potential mental challenge involved in its use are a form of enrichment. That it would take some time to discover the most fitting way to use the novel climbing aid is not inherently an issue in the long term. However, it would be preferred not to create conditions that reduce the ability of the chimpanzees to take advantage of the vertical space available to them even in the short term.

While the ability to climb a novel substrate like the climbing aid may present little barrier to climbing in some chimpanzees, members of the study group may have certain attributes that hinder their climbing on novel substrates. The most critical period of life for developing competency at climbing for chimpanzees occurs prior to adulthood, where locomotor play is thought to be performed in order to develop an individual’s ability to control the movements of their body among the features of their environment (Špinka et al. 2001). Unfamiliarity with the use of a particular substrate type during juvenility could inhibit an adult's comfort level with readily locomoting on said substrate. As Morimura and Mori (2010) reported, chimpanzees who were raised in captivity were less likely to solve problems to achieve a food reward by integrating the use of a new substrate when compared to wild born chimpanzees. Since the captive-born subjects of this study were all adults (ages 28-42 years), their willingness to use a new substrate type may have been stunted, requiring a greater amount of time to familiarize themselves with the new substrate before achieving enough comfort with its use to demonstrate the climbing aid's potential value.

The climbing aid implemented in this study was designed to facilitate safer and less energetically expensive climbing. If safety and energetic concerns are in fact at the forefront of the studied chimpanzees' minds when deciding whether or not to climb on the platform structure, the results presented in this report do not provide evidence that the design of the climbing aid adequately addressed these concerns. The approach taken to design the climbing aid emphasized the relative ease with which a chimpanzee could generate sufficient frictional force between the points of contact of their body and the substrate to support their weight when climbing. While the climbing aid may have made it less difficult to direct one's weight in a direction closer to perpendicular to the surface of the substrate, allowing for the generation of larger frictional forces, this did not address the limits of the coefficient of friction between the volar skin and the surface of the bare wood supports. It is possible that energetic difficulty and safety concerns with climbing bark-less wooden supports could only be adequately addressed by modifying the surface of the wood to provide a texture with a greater coefficient of friction between the substrate and the body of a given chimpanzee. If this were achieved, chimpanzees would need to spend less energy applying force to the substrate at different angles to produce a sufficiently secure connection to the substrate. In this case, fewer balancing adjustments would need to be made to prevent oneself from falling, which would save energy and address safety concerns more completely. Further shortcomings of the climbing aid may be its primary focus on facilitating higher friction between the substrate and the forelimbs. The presence of the climbing aid attached to the sides of the wooden columns may have made it more difficult to grasp or move one's feet along the substrate and in a manner that involved wrapping the feet along the sides the wooden column. This could have reduced the ability of the chimpanzees to create friction between their feet and the substrate unless they altered their climbing technique.

Generating enough frictional force to sustain one's connection to the substrate may not be the only or primary safety concern restricting the chimpanzees' tendency to climb the large wooden columns. In some human climbers, injuries and deaths sustained from falls occur when climbing trees where minimal branches surround the climber (Barss et al. 1984). When there are plentiful branches around an ape's body, they may be better able to arrest their fall by grasping nearby branches when their body's secure connection to the main substrate is lost. Therefore, without the presence of additional supports extending from parts of the platform structure that could be grabbed if the need arose, a chimpanzee concerned with their safety while climbing may not have those fears extinguished.

Elderly chimpanzees in particular have been observed to climb at lower elevations and over shorter vertical distances (Finkel et al. 2022). This avoidance of longer climbing distances would minimize the risk of injury from falls by lowering the amount of time an individual is far away from a strong support that they may grasp onto if necessary, and by offering less chance for them to suffer from exhaustion and experience its accompanying loss of acrobatic ability. Older chimpanzees like the subjects of this study may be averse to climbing vertically for the complete distance between platforms. In this case, the presence of a vertical climbing aid that does not cut the distance between a platform and the next highest resting place would have little benefit to the chimpanzees' tendencies to climb up the vertical columns.

Even when more numerous types of climbable substrates are available to captive chimpanzees, captivity generally eliminates some of the major motivations for climbing that is seen in the wild. Chimpanzees living in conditions consistent with their historic contexts need to climb in order to forage for fruits, hunt monkeys, create and sleep in their nightly nests, and avoid predators. In captivity, the predators are absent, negating the need to climb for one's personal safety. At the same time, the risks of injury associated with climbing remains. Arboreal foraging in captivity is also rarely necessary as food is most often provisioned at ground level and fruiting trees are typically absent from enclosures. Provisioned food may be thrown by caretakers onto elevated spots in an enclosure, but this tactic is both unreliable as a means of consistently providing foods at higher elevations and undesirable as it may exclude certain chimpanzees from partaking in the forage if they are not avid climbers or are unwilling to compete with others at higher elevations. The remaining motivations for climbing that persist in captivity include the need to escape aggressive conspecifics during fights, achieve higher vantage points for viewing within and outside of their enclosure, avoiding conspecifics, occupy favorable resting spots, and engage in general play and exploration. Without a strong enough motivation to climb, any disincentive to do so may be determinative of an individual's tendency to engage in this type of behavior.

If fighting is a major motivation for climbing among the captive chimpanzees of this group, changes in social dynamics and tendencies to participate in conflicts would also have effects on observed frequencies of climbing behaviors. After the group's reintroduction to their typical enclosure, the group exhibited fewer fights involved in platform level changes on both platform structures in their outdoor enclosure. When a group is experiencing high levels of intragroup conflict, one of the behavioral management strategies that Chimp Haven employs is to cycle the group into a new enclosure, which seems to have a pacifying effect on their behavior (Chimp Haven staff, personal communication). While this study was not able to fully consider social dynamics in the group, I anecdotally observed an increase in social play and sexual interactions after the group's return to their typical enclosure. Data on substrate use in this study included contact with other chimpanzees, which corroborated this observation as contact with other chimpanzees increased after the group's return to their typical enclosure (see Figure 4.3.2.3).

As outlined by Duncan et al. (2013) and Videan and Fritz (2007), chimpanzees may employ either a conflict avoidance strategy or tension reduction strategy to diminish the chance of fights occurring, particularly when under conditions of spatial restriction. The conflict avoidance strategy involves individuals spreading out and avoiding particular chimpanzees with whom they may expect to experience conflicts. The reduced frequency of fight-related elevation level changes occurring on the platform structures throughout the study may point to the absence of strong social conflict that produces the conditions for greater expression of climbing behaviors. The return of the group to their typical enclosure from the smaller temporary one may have pacified existing social tensions, reducing the need to use the platform structures not just during fights, but to spread out within their enclosure to avoid excessive interactions with conspecifics that may lead to conflicts. That the use of the south platform was reduced to a greater degree than the north platform may derive from the fact that the north platform was used overall more often than the south platform during both periods of the study. If chimpanzees occupy the elevated platform levels as part of a strategy of conflict avoidance, it may be expected for them to occupy their preferred platform structure at greater rates during times of low social tension and spread to the less preferred platform structure only motivated by greater social tension. Under a conflict avoidant paradigm, occupation of the preferred north platform structure would grow at a slower pace with increasing social tension because increased density of chimpanzees on the north platform structure would also increase the chances of conflicts erupting. Increased rates of occupation for such portions of the enclosure would diminish with increasing social tension.

The tension reduction strategy highlighted by Aureli and De Waal (1997) predicts that under stressful conditions like increased spatial density, group members would associate more closely with each other, engaging in affiliative behaviors to reduce social tensions. If this model is extended to lower spatial density environments, then more stressful conditions that produce greater social tension would also lead to chimpanzees restricting their space use in order to associate more closely with others and mend damaged relationships. When social tension is high, failure to seek reconciliation could lead to detrimental increases in the rates and severity of fighting (Koski et al. 2007). While enclosure changes are typically considered to be a form of enrichment, this practice may simultaneously present a point of stress for the group. If this stress or other concurrent stressful events were impacting the study group upon their reintroduction, irritability may have increased social tension in the group, requiring closer physical association and affiliative behaviors to address tensions. The group would then be less likely to spread out among the platform structures, particularly on the less preferred south platform structure. The increased contact between chimpanzees reported in this study (see Figure 4.3.2.3), supports this interpretation, as does the observed decrease in fight-related elevation level changes (see Table 4.1.4).

It is difficult to assess completely the impact of the climbing aid versus the effects on stress and social dynamics of the group's reintroduction and how these factors interact. The stress of novelty from the climbing aid could contribute to the stress and social tension in the group, even though it was designed to facilitate easier climbing and permit the chimpanzees to spread out if they choose, thus reducing the social tension associated with high spatial density. Greater reductions in the rates of level changes involved in fights on the south platform structure compared to the north platform structure may point to the chimpanzees' distrust of the novel climbing aid for use during the high-risk, rapid locomotion involved in fights. Unfortunately, I was not able to record the frequency of fights throughout the entirety of the enclosure, so it is not certain if this reduction in fight frequency on the platform structures was reflective of the overall rates of conflict throughout the enclosure. Restricting the use of the platform structures during fights may not be preferred if chases involving climbing provide a greater chance for targets to escape without severe injuries. However, that the north platform structure also saw rates of fighting decrease suggests that the larger trend was toward a reduction of fighting after the group's reentry into the study enclosure.

Given that the space use of chimpanzees depends on the space use of other individuals (as in Mitani and Amsler 2003), additional social effects may have also played a role in the observed slight difference in reductions in use of the two platform structures. Stochastic elements unrelated to differences in the platform structures could have influenced the decisions of key individuals on how they used parts of their enclosure at a given time. If a subject whom numerous chimpanzees tend to avoid or associate with chose to use a specific part of their enclosure for any given reason, this would alter the space use patterns of other group members regardless of the relative energetic and safety value of the climbing aid compared to bare columns. Even if the majority of individuals did prefer the use of the climbing aid, avoidant behavior by key individuals who did not prefer the climbing aid could cause attracted conspecifics to use the experimental platform structure to a lower extent.

Anecdotally, Maggie was the only chimpanzee I observed who attempted to ascend onto the second level of the south platform structure but reversed course upon seeing the climbing aid. Her initial aversion to the climbing aid may have emerged and persisted for reasons ranging from general neophobia to physical discomfort as a product of her visible spinal alignment issues. Maggie could be considered a key individual especially during the second period of the study, as she was in estrous. During her estrous state, Maggie grew a very large sexual swelling that made her a highly valued social partner for some of the members of the group (personal observation; personal communication with Chimp Haven staff). This may have impacted her behavior in addition to the behavior of other group members. Jake in particular is known to show a special interest in Maggie, often sitting in doorways during shifting (moving chimpanzees from one place to another) to prevent her exiting without interacting with him. It is not difficult to imagine that changing sexual, mental, or physical states among certain individuals would affect the space use behavior of interested group members. In this particular case, if Maggie discriminated against climbing the south platform after the climbing aid was installed, interested males like Jake and Shone may have changed their space use in the enclosure to attain closer proximity to Maggie. Changes to the space use patterns of these two high ranking males and one high ranking female would result in additional changes to the spatial patterning of other group members. For example, an individual who was prone to associate with Jake or Shone would also utilize the enclosure in similar ways to Maggie, Jake and Shone. Individuals who were prone to avoid Jake or Shone would no longer need to occupy portions of their enclosure that these two rarely occupied.

Notably, as with other substrates, certain individuals were more prone to use the climbing aid than others. Rates of use for the climbing aid by individual were difficult to assess with focal animal data as climbing on the platform structures generally occurred too infrequently and for too short of durations to capture during scans. The video footage used to determine platform level changes during the study were not of sufficient quality to reliably identify most individuals based on their appearance. The majority of the few focal animal observations that did include contact with the climbing aid were attributed to Marsha. Marsha and Shone were noted to anecdotally interact with the climbing aid most often during the period of the study after its introduction, and after the study's conclusion (Chimp Haven staff, personal communication).

Other external factors may have played a role in altering the behavior of the collective or particular chimpanzees in the group in a manner that produced downstream effects on their group-mates. Events occurring in other nearby enclosures are known to have an impact on the behavior of captive chimpanzees within audible distances (Baker & Aureli 1996). Such events could arouse chimpanzees in the study enclosure, or otherwise alter the behavior of individuals who are interested in viewing these events in other enclosures. In this study, Apache was notable for seeking to watch other nearby groups of chimpanzees, particularly when agonistic conflicts were actively occurring in these groups. The observed high frequency of Apache sitting on his buttocks with his arms in suspension (as in Figure 4.2.1.1) occurred as a part of this behavior of watching adjacent groups of chimpanzees. Peewee and Simpson were known to interact frequently with care staff when they were present (Chimp Haven staff, personal communication). Shone and Fancy sometimes followed me while I was collecting focal data on other individuals. Particular subjects had established relationships with particular members of Chimp Haven's care staff and would seek to interact with them when given the chance (Chimp Haven staff, personal communication). In general, many human-centered events occurred in the mornings during the times that data were collected in this study. Chance events during this period likely impacted space use within the study enclosure.

Daily temperature, humidity, and sun exposure may have been factors in how individuals use their enclosure. As seen in Table 4.3.1.4, individuals showed distinct tendencies for occupying spots in their enclosure based on their exposure to sunlight. When heat indices were high during the study, related discomfort could cause individuals to change their positional behavior tendencies (Kosheleff and Anderson 2009; as in Kovács et al 2018), exhibit more irritability, or occupy cooler spots with less exposure to sunlight (Kosheleff and Anderson 2009; Ontl and Pruetz 2020). Alternatively, a high heat index could cause an individual to conserve energy to minimize the chances of suffering heat exhaustion during intense bouts of locomotion

(Bak et al 2017; D'Anci et al 2006; Kosheleff and Anderson 2009; Nybo et al 2014). The occurrence of either of these models for changed behavior as a function of heat intensity could be in play at different times depending on the context. If subjects were experiencing some degree of heat-related lethargy on particular days during this study, they may have avoided expending energy climbing. If a high heat index increased social tension individuals may have associated more closely with others in attempts to reduce tension, or may have avoided occupying elevated portions of the enclosure due to the higher risk of severe fall injuries occurring during conflicts at high elevations. Additionally, rainfall or dew collection during this study could have affected the tendency of chimpanzees to climb when supports were slippery. However, rainfall was only observed on platform structure use footage during one day before the installation of the climbing aid and one day after installation of the climbing aid.

5.2 Positional Behavior Profiles

The individual and collective positional behavior profiles, and tendencies for substrate associations present in this report provide evidence of the unique tendencies for how individuals engage their bodies within their environment. The wide array of ways that a subject's positional behaviors manifest could point to different and changing states of wellbeing among chimpanzees (Hopper et al. 2022). By collecting data that can be combined into a number of positional categories, one can identify motifs of expression that can be ascribed value based on their known association with improved or hindered physical or mental wellbeing. Such associations would need to be validated against other welfare measures but may be key to understanding the ways in which an ape's physical environment and positional behavior expression reflect and contribute to their physical health and internal mental states. This information could inform captive management practices to address issues of captive welfare in chimpanzees.

As suggested by Neal Webb et al. (2023), rates of locomotion may be a useful measure for determining welfare in chimpanzees. Locomotion frequency for the subjects of this report varied from 3.75% of time (Cliff) to 28.25 % of time (Peewee). This metric is indeed very sensitive to change depending on the identity of the subject. Validation of this measure was beyond the scope of this thesis and would provide more insight into the value of such a metric in determining the relative welfare states between different individuals. It may be the case that displacement and fear of conspecifics can motivate some increases to locomotor behavior, or that stoic sedentism could act as a social signal displayed by high-ranking individuals. Such factors would confound comparisons of welfare states between individuals at one time. Changes in tendencies for locomotion as a function of other enclosure or management practice changes, as were reported in Neal Webb et al. 2023, may entail a more suitable purpose for the welfare value of locomotion rates. While the activity budgets of individuals may differ based on rank, personality, and long-term behavior patterns such that the relative differences in locomotor behaviors between individuals persists through time, the changes in locomotion frequency over time within an individual could still indicate changes to the individual's state of wellbeing.

Given the evidence for broad positional categories being associated with particular welfare states, more detailed positional data could also be indicative of mental welfare with greater specificity. As an example, the tendency for individuals to engage in limb use motifs entailing contradictory use functions, such as when one forelimb is out and the other clings or suspends from another substrate, may indicate that a chimpanzee is attempting to rest, but is expecting the need to change postures at some point. This may suggest a fear of other conspecifics or a need to address differences in resting postures and substrate use between captive and wild chimpanzees (Stewart et al. 2007). Other positional motifs, like self-clasping, which involves a subject grasping onto another part of their body, may signal poorer welfare (Birkett and Newton-Fisher 2011; Lopresti-Goodman et al. 2013). Engaging in self-clasping may indicate that a subject is less willing to engage their limbs with the surrounding substrates, and the subject may have a hindered motivation to fully engage their limbs as a part of their postures.

Posture motifs could also be useful for interpreting social signals (Hobaiter and Byrne 2014). The self-clasping displayed by Cliff and Novella may signal that these individuals are not a threat and are not interested in encroaching on the space of others. Sitting and squatting showed greatly different rates of expression among individuals, and may indicate the degree to which one is willing to change posture from their current position, given that their body weight is able to rock over the point of contact between the feet and the ground. Differences in body orientation between individuals reveals that female chimpanzees were more likely to orient their bodies in pronograde manners, while males were more likely to orient their bodies in orthograde manners. As has been suggested for female panins previously (Demuru et al. 2020), the pronograde orientation may act as a sexual display. The orthograde orientations characteristic of males, with legs extending further out or held in the mid-compression state could similarly operate as sexual displays, especially since they leave male genitalia vulnerable, despite the tendency for extremely aggressive opponents to target these body parts when given the opportunity (Watts et al. 2006).

At this time, the limited amount of data collected, and lack of applied validation measures prevents my declaration of the welfare implications of any particular positional motif, as doing so would largely constitute speculation. However, the level of detail presented by the data collected in this study points to the potential for the occurrence of such motifs under particular circumstances to correlate with particular internal states.

Positional behavior profiles may be used to identify limitations in an individual's positional repertoire. Identifying these limitations among the categories of the larger positional categorization schemas is not especially useful when considering the limited amount of data collected for this report. It may be more useful to examine differences in limb and axial body use tendencies to identify positional motifs in which a particular individual fails to engage.

Persistent medical issues could hinder the positional abilities of captive chimpanzees, leaving evidence of their existence in the collected positional behavior data. Comparing the rates of occurrence for particular positional motifs with known medical issues was beyond the scope of this study. Subjects' medical records were not considered, and their contents were not linked to these positional motifs, but the potential for doing so in future welfare reports could aid in the identification of the signifiers of physical ailments. This may allow for the earlier detection of maladies, facilitating for their proactive treatment by medical interventions.

While focal data were not collected on subjects' spinal alignments, I anecdotally observed that Peewee's back exhibited a relatively high degree of kyphosis, and Maggie's back appeared stiff compared to the other chimpanzees (personal observation). Potential issues of spinal alignment were not confirmed with medical staff or medical records in this study. Interestingly, these two individuals were the two most likely to engage in locomotion during a given scan (see

Table 4.2.1.2). With locomotion occurring at rates of 28.25% of scans for Peewee and 23.38% of scans for Maggie, these far exceeded the average locomotion rate of 11.7% of scans for the entire group. Higher rates of locomotion in this group may signify physical discomfort and a need to alter one's spatial position to prevent strain on parts of one's body. If locomotion rates at such high levels were indicative of spinal issues, other subjects, like Marsha, who engaged in locomotion during 20.89 % of scans, may also be showing early signs of ailments to her back. Alternatively, the typical threshold above which high rates of locomotion are representative of physical impairments of the spine may lie between the rates attributed to Marsha and Maggie.

Peewee, Maggie and Simpson, were the chimpanzees most likely to express the motif of holding both arms in compression. Peewee and Simpson were the most likely to engage this motif while sitting, Peewee and Novella were the most likely to engage this motif while squatting, and Peewee and Gary were the most likely to engage one arm in compression while squatting. The nature of these positional motifs, along with Peewee's relatively more kyphotic spinal curvature compared to other chimpanzees (personal observation), point to his need for employing his arms to keep balance as his arched back places his head in front of his center of gravity. The weaker expression of these motifs in other individuals may suggest similar balancing issues during scans, which may be result of similar developing spinal issues, like sarcopenia (Gadelha 2018), or a general lack of balancing competence. In this case, enclosure elements and captive management practices may best be modified to improve balance, potentially by employing some manner of rebound therapy (Daneshvar et al. 2019). An additional signal of Peewee's condition may be his exaggerated tendency to lean on his forearm while sitting on his buttocks. Such a posture would likely be uncomfortable for a non-kyphotic individual, so observations of this posture's occurrence could be useful for the early identification of mild cases of clinical kyphosis. It may be especially important to consider the positional behaviors related to kyphosis when monitoring the health of aging chimpanzees if the development of age-related kyphosis as a result of sarcopenia is as common a problem for captive chimpanzees as it is for humans (Soylu et al. 2021).

The differential use of both sides of an individual's body can also point to injuries affecting one forelimb or one hindlimb, but not the other. Jake expressed differential use of his legs, likely because he was fully missing all toes but his hallux on his right foot and retained his hallux and two other toes on his left foot. Consequently, his right leg was held in the bent-compression state more often than his left, while his left leg was more often laid out or clinging to an additional substrate compared to his right leg. This points to his right leg, with its lack of any toes besides the hallux, being used to supporting his body weight, while his left leg extended further from his body to maintain his balance. While it is readily obvious by looking at Jake that he is missing many of his toes, this information can again provide insight into the changes in positional behavior that may occur as a result of such injuries. An injury that causes failure for an individual to grasp with one of their feet may lead to similar patterns of whole leg use. As such, recording the positional tendencies of an individual with a known and apparent injury could help to provide a sensitive measure of functionally similar impairments that are more difficult to notice using the naked eye.

Shortly before the beginning of this study, Apache was reported to have lost some mobility in his left leg, which was diagnosed to stem from cellulitis (Chimp Haven staff, personal communication). As shown in Figure 4.2.2.6, Apache engaged his right leg in the bent-compression state to a greater degree than his left leg. He also clasped onto his body more often with his right leg and clung to additional supports more often with his left leg. Sidedness was present in the hindlimb use of other individuals who had no known leg injuries. However, given that Jake was the only other subject who expressed sidedness in hindlimb clinging, it may be the case that differential hindlimb clinging is specifically employed to address asymmetries in hindlimb impairment status. While data were not recorded for enough time to effectively monitor the recovery of Apache's injury, its detectable presence suggests that longer term changes to sidedness of this positional motif could be useful for future captive management programs to assess recovery of similar mobility impairments with subtle outward effects.

In addition to monitoring one's recovery from physical ailments, changes to positional motifs associated with medical issues over time could also be used to monitor rates of age-related degeneration as a result of a given malady. Even before the onset of notable muscle degeneration with age, deficiencies in the manners by which one interacts with their environment could lead to eventual atrophy or injury (Zizzo 2021). As such, it may be especially pertinent to consider how an individual may fail to use their limbs, particularly in comparison to typical rates of expression for positional motifs, or the expression of positional motifs by healthy conspecifics.

This thesis provides further evidence for the potential value of considering behavioral diversity when assessing welfare but highlights the need for further refinement to these metrics. Individuals demonstrated discernible differences in positional diversity. These scores provide quantitative metrics that may be validated in future studies to determine the degree to which they correlate with current understandings of welfare status. Validation is an essential step that must be taken before positional diversity can be used on its own to infer welfare. This may be done via comparisons to non-invasively collected stress hormone and immune factor analysis, rates of positive and negative behavioral welfare indicators, and comparisons under external conditions thought to produce positive and negative welfare states. This is not only necessary to determine the efficacy of considering positional diversity generally, but would provide insight into which positional categorization schemas would produce the positional diversity scores most correlated with particular internal states and physical health qualities of interest (as in Hall et al. 2021).

Positional diversity scores could be used to prioritize changes to captive management practices that seek to improve conditions for keystone individuals or those who need the most immediate attention to improve their positional signifiers of wellbeing. Addressing the positional deficiencies of individuals with the lowest positional diversity scores could in the aggregate improve the overall wellbeing of captive residents at a given institution. As such, diversity scores can offer a practical means of improving the lives of captive individuals in the most cost-effective and directed manner.

The diversity scores generated for this thesis varied greatly based on the positional modes and classification schemas considered. Consequently, the degree to which a given score correlated with others varied. There was relatively higher agreement between positional diversity under the Pos1 schema and the hindlimb-focused Pos5 schema when compared to the lower agreement between positional diversity under the Pos1 schema and forelimb-focused Pos6 schema. While diversity scores relying on forelimb use to a greater degree may still be employed, this may suggest that the forelimb use ethogram could be split to provide a similar level of specificity for both forelimb and hindlimb use types. It may be desirable to develop positional classification schemas that produce similar relative diversity scores in the name of consistency so that actual positional diversity can be accurately represented. However, the simultaneous consideration of multiple positional diversity scores that prioritize particular positional motifs could also be of use. As this study demonstrates, despite the lack of agreement between positional diversity scores relying on such classification schemas as Pos3 and Pos4, the chimpanzee characterized by the lowest diversity score across the different classification schemas was Cliff. Low diversity scores among disparate means of positional categorization could suggest a degree of reliability to the idea that Cliff indeed expressed the lowest degree of positional diversity in this study. This may provide stronger evidence of the result compared to if Cliff presented the lowest positional diversity among only one classification schema. The necessity to standardize behavior categories used to generate behavioral diversity scores (Cronin and Ross 2019) was addressed indirectly in this study. Rather than committing to and advocating for one set of positional categories when collecting data, I suggest that the ethogram consisting of positional elements of the limbs and axial body utilized in this study could be standardized, and that these could be combined in a number of ways to generate the positional classification schemas ultimately used to calculate the diversity of overall positional modes. The ethogram employed in this study incorporates aspects used to distinguish positional behaviors in other ethograms (Hunt 1996; Sarringhaus et al. 2014; Thorpe and Crompton 2006) and may therefore find agreement among those familiar with these previously employed classifications.

5.3 Enclosure Space and Substrate Use

5.3.1 Enclosure Zones and Sunlight Exposure

Data on enclosure zone use and sunlight exposure reveal individual patterns of space use that could be of critical importance for addressing issues of psychological and physical wellbeing in captive chimpanzees. If the hypothesis that sudden cardiac arrest in captive chimpanzees is related to deficient vitamin D production (Moittié et al. 2022; Strong et al. 2020), data presented here could point to those most at risk of experiencing heart failure. An insufficient number of trials were performed over an adequate period of time to fully ascertain individual tendencies in sunlight exposure, but preliminary data suggests Cliff, Coco, Dino, Shone, Simpson, and Zort were the least likely to experience direct sunlight. Shone spent the least amount of time indoors of any subject. Despite this, he may not be considered at high risk for deficient sunlight exposure since he spent much of his time outdoors, albeit in the shade (see Figure 4.3.1.4). Coco and Dino were both the most likely chimpanzees to occupy indoor spaces and the least likely to experience partial shade. The tendency to fail to experience full sunlight for the males in this study is consistent with reports on the increased likelihood for captive male chimpanzees to experience sudden cardiac arrest (Lammey et al. 2008; Strong 2017).

Addressing this issue could involve utilizing the collected data on substrate preference presented in this thesis. While Cliff was one of the two chimpanzees most likely to occupy indoor space, he also showed a strong preference for occupying wooden platforms and leaning against the sides of wooden columns (see Figure 4.3.2.1). This suggests that there could be a benefit to providing more outdoor spots to sit and lean against wooden columns in order to encourage Cliff to occupy areas with greater sunlight exposure. If the texture of the wooden platforms are desirable to Cliff, integrating small portions of wooden platforms into the outdoor enclosure at ground level may also encourage its occupation. Given that use of the grass substrate and yard zone of the enclosure were minimal for most chimpanzees, incorporating wooden platforms at ground level may make occupying the center of the outdoor enclosure more appealing and encourage the use of adjacent enclosure features. Cliff was also the chimpanzee most likely to sustain contact with conspecifics during a given scan. This suggests the benefits of encouraging other valued social partners to spend time resting or grooming in outdoor spaces with more sunlight exposure as a way to motivate Cliff's outdoor space use.

Coco was similarly prone to occupying indoor spaces and showed a strong preference for the concrete ground and concrete wall substrates. He was also the chimpanzee most likely to incorporate firehoses into his postures. If the preference for occupying indoor spaces is derived partly from its substrate makeup, constructing a concrete wall and ground section within the more central outdoor enclosure, complete with metal shelves and fire hose, could make its occupation more attractive to Coco. Additions to the center of the enclosure could also be incorporated into intermediate areas between the center of the yard and preferred indoor spaces so that these spots can be easily reached without requiring locomotion on less preferred substrates.

If any preference for the indoor spaces among the subjects could be derived from their aversion to direct sunlight, particularly during times where the outdoor heat index is high. This may be addressed by providing more shade and partial shade to preferred areas of the outdoor enclosure. This would limit the subjects' exposure to direct sunlight, while also providing enough reflected sunlight from their surroundings to still stimulate vitamin D production (Macdonald 2013). Alternatively, the indoor areas of the enclosure could be modified by directing mirrors or fiber optic cables to deliver more sunlight into spaces that otherwise receive light mainly from artificial light fixtures (Song et al. 2021).

5.3.2 Substrate Use Profiles

Individual substrate use profiles may be utilized by interested parties to identify limitations in the willingness of individuals to use particular substrates. As discussed previously, such unwillingness may be rooted in neophobia and anxiety toward substrates with which one is unfamiliar. Strong affinity for certain substrates or the failure to use a particular substrate may also point to a tendency to limit one's enclosure use to only a small set of familiar experiences (Duncan et al. 2022). As such, substrate affinity profiles may be used to determine the degree to which subjects limit their substrate use or to track changes in these tendencies over time. Diversity in substrate use can be calculated, as in Table 4.3.2.3, to compare individual propensities for using a variety of substrates. Here, we would consider Zort to have the least diverse substrate use profile with the least even spread, followed by Coco. In contrast, Pumpkin and Apache expressed the greatest relative diversity in substrate combination use, while Peewee and Apache expressed the greatest relative diversity in general substrate use. Based on this data, it would be recommended for efforts to be put toward expanding the diversity of substrates used by Zort and Coco. Furthermore, such data could be used to assess differences between the substrate use patterns in different groups in similar enclosures, or to assess the quality or degree to which chimpanzees take advantage of the features present in different enclosures.

The Shannon diversity index calculated for substrate use may also be used to determine the degree to which a given chimpanzee is open to incorporating different available substrates into their repertoire of regular environmental interactions (Hopper et al. 2014; Massen et al.

2013). This may compliment metrics employed by other studies for assessing personality traits that also reflect an individual's tendency toward neophobia or general aversion to the unfamiliar experiences. Such issues would require attention in order to improve the efficacy of enrichment provisioning to subjects and improve their general diversity of experiences. Increases to a chimpanzee's willingness to engage with a multitude of substrates could signify the growth of a mindset that finds variety in experiences more acceptable and seeks less homogeneity. Low substrate use diversity scores may suggest the need for captive management programs to find ways of cultivating the ability for a subject to use enclosure features currently under-represented in their substrate use profile. Thus, the priorities for adding structures into an enclosure may be informed by the failures of particular chimpanzees to use particular substrates.

Strong departures from average rates of substrate use could also be identified regardless of an individual's substrate use diversity score. This is especially pertinent if different values are assigned to different substrates, as would be the case when considering the positional behaviors associated with the substrates. Data presented here suggest that Zort, Coco, and Simpson have the strongest tendencies to occupy the concrete ground. If this condition is undesirable based on the potential impacts of the substrate on the morphology of the chimpanzees' joints (Lewton 2017) or the potential for disease transmission on concrete surfaces (Leinwand et al. 2021), it would be necessary to identify those who are most likely to occupy the concrete ground in order to mitigate any potential negative effects of its use. Jane, Maggie, Novella, and Pumpkin occupy the concrete ground at lower rates than average for this group, opting instead to use the metal shelves and metal mesh around the perimeter more frequently than most other group members (see Table 4.3.2.1). This may signify its own issue if these individuals find it necessary to avoid potentially aggressive conspecifics who are more likely to occupy the concrete ground where targets of aggression may be more vulnerable to attack.

The tendency for female chimpanzees to show stronger affinities for the perimeters of enclosures is consistent with previous reports and common caretaker observations (Traylor-Holzer and Fritz 1985; Chimp Haven staff, personal communication). Metal mesh substrates are most common around enclosure perimeters, and their climb-ability makes them analogous to the easily climbable portions of arboreal environments.

In both captive and wild contexts, female chimpanzees are more likely than males to occupy arboreal environments (Doran 1996; Fultz et al. 2023). This phenomenon may be related to the smaller average size of female chimpanzees (Doran 1996). It is notable that female chimpanzees in wild contexts seek refuge in elevated arboreal spaces when they are the targets of aggression and sexual coercion from male members of their group (Watts 2021). When feeding within fruiting trees, wild female chimpanzees are reported to either engage in minimal or more passive forms of aggression to regulate the distribution of group members among feeding sites of different degrees of quality (Houle and Wrangham 2021). Other sympatric frugivorous primate species will similarly avoid proximity to more dominant species feeding in the same tree, even in the absence of preceding aggression (Houle et al. 2010). Given that chimpanzee falls from elevated heights occur most often during fights between individuals (Boesch and Boesch-Achermann 2000), chimpanzees may reasonably avoid engaging in aggressive actions in elevated spaces in order to curtail the risk of injury or death associated with a fall. Occupying arboreal spaces at greater heights also presents an energetic barrier that could deter an aggressive chimpanzee from pursuing the target (Pontzer and Wrangham 2004), or may limit the aggressor's ability to position themself in a manner that allows them to gain leverage against a stable horizontal substrate to inflict as severe of damage on the target (Carrier 2007). The tendency of female chimpanzees to occupy arboreal contexts and their artificial analogues of elevated spots along metal mesh substrates may therefore operate as a strategy of avoiding severe aggression from male conspecifics.

Furthermore, in captivity, occupying perimeters would allow an anticipator of aggression to selectively focus their attention only in the limited number of directions toward the interior of the enclosure. In this way, they are protected from attacks by chimpanzees approaching from the directions along which the distance between themselves and the perimeter is minimal. They could then react more quickly to approaching aggressors and would be less likely to be caught off guard from an attack. Additional negative effects of a tendency toward occupying the perimeter of an enclosure include the avoidance of other portions of the enclosure, which may limit the effect of enrichment efforts meant to provide new experiences to these individuals.

Informed modifications to enclosure structures and arrangements may be made based upon inhabitants' substrate preferences in order to improve the welfare of resident chimpanzees through their enclosure use. As in Ross et al. 2009, an understanding of the rates of substrate use and preference for a given group of chimpanzees could be used to make more desired enclosures with effectively usable features. In this study, the perimeter and indoor areas of the enclosure were used most often by the subjects. With the notable exception of Marsha, female subjects were disproportionately more likely to occupy the perimeter of the enclosure, opting to use the metal mesh and metal shelves at greater rates than the average for this group. This pattern of enclosure use represents a limit to the effective space available to these members of the study group. If these individuals tend to restrict their space use to areas in which metal mesh substrates are present, it would be beneficial to extend these substrates into additional portions of the enclosure. The addition of metal mesh substrates onto the platform structures in the central portion of the enclosure may help to provide a substrate that is more familiar to these individuals and permit a style of climbing that more subjects are practiced at performing. This strategy for increasing enclosure space use could benefit those who restrict their occupation to metal mesh and shelf substrates, but it may also provide benefit to other subjects who are not as likely to engage with these substrates. If individuals like Marsha, Cliff, Peewee, Gary, Shone and Simpson are prone to occupying the platform structures, the periods of time in which they spend in these enclosure zones precludes their ability to interact with the metal mesh substrates. If these individuals tended not to engage with metal mesh, but were willing to when it is present, the addition of mesh substrates in frequented areas of the enclosure could increase these subjects' overall substrate use diversity. This approach may also increase the ability of chimpanzees to make use of vertical space in the enclosure because of the integration of a more prevalent, familiar, and easily climbable substrate into this portion of their enclosure. Installing metal mesh among the platform structures may also have the effect of homogenizing the enclosure in a way that eliminates the need for subjects to explore different ways of climbing apart from the familiar use of metal mesh. However, if greater integration of disparate substrates is achieved, this may also train subjects to be willing to use more substrates in their enclosure to greater degrees. This recommendation is consistent with the conclusion made by Soubiea (2017) that artificial substrates should be integrated into the more naturalistic portions of an enclosure.

Other preferred substrates may similarly be used to encourage use of a particular area of the enclosure by interested individuals. Maggie, Marsha, and Pumpkin were the chimpanzees with the greatest tendencies to lie in hammocks. A more usable enclosure for these chimpanzees in particular may be achieved by incorporating hammocks into additional parts of the enclosure. However, at the time of this study an additional hammock was present on the enclosure's central canopy structure which was left unused throughout the study. This points to the limitations of considering only substrate use preferences to make determinations for the additions of these same substrates. Rather, it may be necessary to consider other features of the cases in which those substrates are used. The fact that the central canopy structure was only rarely used suggests that the tendency to occupy nearby locations is a prerequisite for using the hammocks. As such, motivating the use of a particular feature of the enclosure may require the inclusion of preferred substrates around it.

The preferences of Gary, Shone, and Simpson for the use of wooden ramps could similarly be used to encourage further occupation of particular areas by these subjects. By installing additional angled wooden platforms into the enclosure, it may be possible to encourage these individuals to use these familiar substrates in new ways, with the potential effect of drawing these subjects away from the main ramps leading to the platform structures. Voids in occupation of the routes leading to particular features of the enclosure could allow for other group members to take advantage of these features to greater degrees than if doing so required interrupting the personal space of individuals with whom a given chimpanzee may have a contentious relationship.

Additional enclosure modifications could be made based on known patterns of enclosure use in order to encourage an individual's engagement with rarely used substrates. In this study, Apache was prone to sitting with his arms suspended from metal mesh. While not recorded as part of this study's ethogram, this posture was performed particularly when Apache sought to view groups in nearby enclosures who were experiencing aggressive conflicts. If a more preferred vantage point for viewing these nearby groups could be provided to Apache, substrates with which he rarely engages, like a hammock, could be incorporated into this vantage point. Such tactics may help to increase a given individual's willingness to engage with novel substrates by providing them with the choice to do so while also making performing the action a positive experience.

For chimpanzees like Pumpkin, who expressed minimal rates of wooden platform use, but high frequencies of metal shelf and hammock use, wooden materials could be incorporated in locations adjacent to preferred shelves and hammocks. This may make this substrate more appealing and encourage its use in other areas of the enclosure as well. While insufficient evidence is available among the subjects for the persistent fear of interacting with any given material, the addition of functionally equivalent enclosure features made out of different materials may provide an enriching experience that could broaden a chimpanzee's concepts of acceptable substrates on which to reside.

5.4 Link Between Substrate Use and Positional Behavior

Limitations in and unhealthy expressions of positional behaviors may be addressed by considering the ways in which positional behaviors are expressed as functions of the substrates that a subject associated with while engaging in the behavior. If a chimpanzee rarely expresses a particular positional motif thought to be beneficial to their overall physical health, then it may be desirable to incorporate into their enclosure in greater abundance the substrates most likely to result of the desired positional behavior.

As an example, Cliff, Peewee, Dino, Zort, and Shone all demonstrated lower than typical rates of incorporating arm suspension into their postures. Failure to express this motif may diminish the physical capabilities of the individuals to engage in these behaviors through the loss of muscle mass and flexibility required to perform such actions. If these individuals fail to regularly engage their arms in suspension during locomotion as well, any eventual need to perform this action may result in higher rates of injury or a generally diminished propulsive ability. For Peewee, the failure to engage his arms in suspension may again derive from his back's higher degree of kyphosis (personal observation), which may make extending his arms above his shoulders physically uncomfortable or ineffective. Failure for a subject to engage their arms in a suspensory manner may indicate the need to add substrates that are most likely to produce the conditions for suspensory postures or locomotion. Of the substrates considered in this study, arm suspension was most likely to occur in the presence of metal bars, metal shelves, metal mesh, and metal chains. Efforts to increase suspensory behaviors would involve installing more of these substrates within the group's enclosure. Given the known preferences for enclosure area use and substrate use, it would be recommended to install the forelimb suspension associated substrates around other preferred substrates. For Cliff, this may involve the addition of hanging substrates near the sides of wooden columns. For Dino, this may require integrating these supports along the portions of the concrete wall against which he most frequently leaned. These practices may create the conditions that allow for the continued expression of suspensory behaviors into older age, giving subjects the ability to continue to move about in their environment in a species-typical manner.

If the failure of a chimpanzee like Peewee to engage in forelimb suspension cannot be addressed with the additions of substrates alone, physical therapy training techniques could also be employed to try to encourage the presentation of limbs in a way that requires the desired action of that limb (Neal Webb et al. 2020). For addressing Peewee's apparent kyphosis, this may involve encouraging him to extend each arm above his shoulders to the greatest degree possible. For individuals like Apache, Cliff, Coco, Dino, and Jake, their lower rates of squatting and engaging their legs in the bent-compression state may best be encouraged by implementing compliant substrates that require bending one's knees to greater degrees at particular times to maintain balance. If installing such a substrate turns out to be unfruitful or unfeasible, positive reinforcement training may be used to encourage the alternating presentation of their feet in order to encourage balancing on the other in the highly bent form. These types of behavioral interventions may be crucial parts of maintaining physical abilities in aging chimpanzees in the absence of effective substrates to address such issues with similar rates of success.

Data on positional diversity by substrate type could potentially be used to determine which substrates are best able to improve the positional diversity of subjects within an enclosure. As a general rule, present substrates with the greatest associated positional diversity scores would be most likely to produce higher positional diversity scores for individual chimpanzees. In this case, it would be recommended to design and alter enclosures by incorporating the substrates with higher positional diversity scores. However, if substrates with high positional diversity scores reported in this study are characterized by their association with particular types of positional behaviors, a variety of such substrates would need to be incorporated to produce high levels of positional diversity.

Substrates with the highest associated positional diversity in this study included metal mesh, metal shelves, concrete ground, and concrete walls. These were also the substrates most commonly used throughout the study, which may indicate that more diverse sets of positional behaviors correspond to the use of more familiar substrates, but it is also likely that the greater rates of occupation would produce higher diversity scores by chance. When identifying the substrates that are characterized by higher diversity of associated positional behaviors, it is best to consider both the Shannon diversity index (H) in combination with the evenness score (J). Because the metal mesh and metal shelf substrates are linked to higher evenness scores, installing these substrates would more reliably result in greater positional diversity among the residents of a given enclosure. Metal mesh and metal shelves were characterized not only by greater positional diversity, but were also associated with particular positional behaviors that were not characteristic of other frequently used substrates. This points to the potential for additional benefits of incorporating metal mesh and shelves among the naturalistic wooden platform structures in the enclosure that are currently disconnected from any metal mesh.

In order to effectively implement substrates that promote particular positional behaviors and improve general mobility, a groundwork must be laid to determine the effects on positional behaviors of viable substrates. Positional behavior data must be collected on additional substrates and substrate complexes such that more appealing structural additions with targeted behavioral effects are identified and have beneficial impacts on the chimpanzees to which they are provisioned. With enough data collected on the effects of different types of substrates, one may identify the physical and mechanical properties of the substrates in order to better predict the impact of new structures on the positional behaviors of captive chimpanzees. A more detailed examination of the properties of certain structures could also be used to address the failure for chimpanzees to use certain substrates through modifications that make their use more conducive to common positional behaviors.

5.5 Study Limitations and Future Directions

5.5.1 Climbing Aid Assessment

The ability to ascertain the value of the climbing aid in promoting climbing behaviors and vertical space use would be benefitted by several changes to the approach taken in the present study. One of the primary issues with this study was its short duration and limited number of trials performed to assess the use of the platform structures. The need for a greater number of trials performed is especially important when examining variables that depend on rates of locomotion because locomotion accounts for a relatively low percentage of time spent by chimpanzees, and climbing behaviors are only a small portion of the overall rates of locomotion exhibited by chimpanzees (Neal Webb et al. 2023; Sarringhaus et al. 2014), particularly in non-arboreal environments. The rationale for recording stationary positional behavior in this study offers criticism for attempting to evaluate the relative impact of the climbing aid based on a limited number of trials examining an already relatively infrequent behavior. A more complete understanding of the impacts of the climbing aid would be gained if data were collected for longer periods before and after the climbing aid was installed. This would minimize the confounding effects of different short and medium-term events and provide a greater understanding of how the climbing aid and platform structures are used in different contexts and during different seasons or at various temperatures and humidity levels. If video footage data were collected for a greater portion of the day and night, rather than being restricted only to the morning hours, this would provide a clearer picture of how the subjects use the platform structures in total, particularly if the subjects are prone to routines of differential space use throughout a 24-hour period. The expansion of the data collection time window would especially diminish the unpredictable effects of human-sourced events. Additionally, given that Western chimpanzees have been reported to engage in more nocturnal activity while high temperatures inhibit their activity during the day (Pruetz 2018), constructing a profile on how the platform structures are used requires an added understanding of its use in the afternoons, evenings, nights, and early mornings before sunrise.

Using higher quality video footage or subject tracking technology would help to differentiate which chimpanzees were most prone to using the climbing aid and determine its impact on the individual level. Similarly, higher video quality could allow an observer to differentiate the degree and means by which the climbing aid was used as opposed to reporting only data on elevation level changes. Determining the overall value of the climbing aid would also require its implementation into enclosures containing different groups of chimpanzees so that evaluations of the structural modifications are not restricted to examining the set of unique individual patterns of enclosure use in one particular small set of subjects. Installing the climbing aid into enclosures with younger chimpanzees who would be more likely to attempt to climb new substrates could provide insight into the potential of the climbing aid to improve locomotor efficiency and safety. If the benefits of the climbing aid's use are significant under such conditions, efforts could then be made toward installing the climbing aid and promoting locomotion upon it in older individuals.

The potential for individuals to use the climbing aid might be expected to increase over time if neophobia or general unfamiliar object or locomotion style aversion played a factor in limiting the rates at which climbing on the climbing aid occurred. Studies on climbing aid evaluation would benefit from incorporating a familiarization period, after which data on enclosure use in the acclimatized subjects would be collected. Including a training period for the use of the climbing aid may have also helped to familiarize the chimpanzees with its use and value. This could be done by provisioning food rewards on the tops of wooden columns, especially those few without alternative paths of ascension. This motivated climbing of a novel substrate would be a unique and enriching experience, and would allow for the human observer's assessment of the informed chimpanzees' perceived value of the climbing aid, and not just their lack of experience and ability with its use.

Further investigations are needed into changes in behavior, space use, social dynamics, and conflict frequency and intensity upon a chimpanzee group's transfer into another enclosure. Understanding the effects of these events in the absence of major structural modifications would allow comparisons to enclosure reintroductions with such modifications. This would also provide insight into the enrichment value and stress that are potentially associated with enclosure changes, and how these impact the tendencies of individuals to closely associate with each other.

The goals of introducing the climbing aid may have been achieved by altering the manner by which the climbing aid was constructed and installed. It would be preferred for future studies to implement structural modifications in ways that do not interfere as strongly with the already present functional use of features within the enclosure. In this study, extending the climbing aid's to the lowest vertical point on the column segments was likely unnecessary and interfered with the chimpanzee's ability to lean against the columns while sitting in their typical manner. When climbing between platform levels, the climbing aid, while providing handles that the chimpanzees could use to pull themselves up, generally prevented the subjects' hands from wrapping around the side of the bare column as they were used to. Regardless of perceived value of the handhold to humans and other chimpanzees, certain individuals may prefer the option of climbing in their established manner. The bottom of the climbing aid could have been positioned slightly above the floor of the next highest platform to allow individuals to climb using the bare column if they choose.

Alternative designs and approaches to creating the climbing aid may have been more effective. Given that the climbing aid was designed to increase the frictional forces between the chimpanzees' volar skin and the substrate, this may have been better achieved by modifying the surface texture on the climbing aid to increase the coefficient of friction between the climbing aid and the chimpanzees' volar skin. Surface modifications could have been achieved by mechanically denting the surface of the climbing aid, or applying a textured coating of urethane. It may have also helped to incorporate more resting spots along the columns so that chimpanzees may be motivated to climb in order to reach these spots, but would also have secure positions to rest along their ascent if need be. This would also reduce the distance of any falls that might occur while climbing, making the endeavor feel safer to the chimpanzees. Safety concerns could also be addressed by incorporating substrates that project outward from the columns so that these could be grabbed onto in the event of a fall. Finally, if vertical climbing on larger and more uniform supports is generally more energetically expensive (Cartmill 1979; Hunt 1991), a better option for increasing climbing behavior and vertical space use may be to provide a climbable substrate with a more erratic form that may be ascended or descended my multiple strategies rather than only by a vertical climbing gait.

Finally, it is not necessarily the case that the lower use frequency of the experimental platform structure after the climbing aid's implementation means that the climbing aid did not have enrichment or therapeutic value. Physical therapies often encourage actions that are difficult to perform given the physical restrictions of the patient. Reductions in rates of chimpanzees performing therapeutic actions might be expected, including rates of climbing in a manner more akin to species-typical vertical climbing. The evaluation of the climbing aid may not be complete by only focusing on platform level occupation and use frequency. It may be necessary to corroborate such data by examining long-term individual changes in techniques employed by individuals when they do climb after the installation of the climbing aid.

5.5.2 Positional Behavior and Enclosure Space Use

While the results of this study provide a promising direction for understanding the welfare implications of chimpanzees' interactions with their immediate surroundings, several issues hinder the broader implementation of this approach to monitoring and improving welfare. First, the duration of the study, the number of trials performed per individual, and the number of subjects considered were all too few to allow for definitive conclusions or recommendations to be made in this thesis. Given the large numbers of positional categories that can be produced, as in the Pos1 categorization schema, the collection of data over large numbers of trials would be needed to provide more specific insight into the tendencies for chimpanzees to engage in particular positional behaviors. While the implementation of large positional categorization schemas such as Pos1 could eventually provide this specificity, at present there is an inflated impact of recorded behaviors that occurred infrequently and may not be present to such a degree if a larger number of trials were performed.

In order to understand the welfare correlates of expressed positional behavior motifs, similar data need to be collected within multiple study populations. Relative rates of expression for such motifs were compared based upon the average rates of expression for this group only. Chimpanzees show cultural differences in many aspects of their behavior, including the techniques used to interact with conspecifics in their environment (Bonnie and de Waal 2006). It would be reasonable to expect that aspects of their positional behavior and enclosure space use would also be bound by micro-cultural traditions within groups. The internal mental states of chimpanzees within the same group may also be bound given the importance placed by chimpanzees on sociality. Furthermore, the general baseline for rates of welfare-related positional expressions among chimpanzees is unlikely to be represented by one group of sixteen individuals. Expanding the collection of positional data using a similar ethogram would aid in identifying typical rates of positional motif expressions, and validation with other established welfare metrics and known medical issues would help to determine ideal rates of positional expressions that signify greater mental and physical welfare. However, even this would depend on the standard expected rates of expression in captive individuals. It may be difficult to record data among wild subjects with the level of detail required to make comparisons to captive individuals given the larger range of spatial positioning that is available to non-captive chimpanzees. However, recording greater detail in posture data may be advantageous in captivity under the assumption that different captive chimpanzees express healthier patterns of certain positional behaviors compared to others. As such, splitting positional behavior into many parts could allow researchers to develop goals for improving welfare in any given captive chimpanzee by focusing efforts on creating experiences that result in the reduction of negative positional behavioral indicators of welfare. Methods for collecting and analyzing data need to be refined and validated with established welfare indicators before the exact positional behavior ethogram can be recommended for widespread use among populations of chimpanzees that would allow for welfare comparisons to be made based on positional expressions.

It would also be advantageous to have the capacity to collect positional data simultaneously with other welfare-related behavioral data that is already being collected, specifically those relating to social interactions and other relevant contexts. However, this may overload the individual collecting such data. Incorporation of detailed limb and axial body element use into data collection ethograms requires modification to reduce the difficulty with which one can collect such detailed behavior in a short amount of time. Under ideal and unrealistic circumstances, welfare-focused captive management programs would collect all possible data for each chimpanzee at all times on stress hormone concentrations, positional behaviors, and welfare-related social and stereotypic behaviors. However, a mixture of tactics for inferring different aspects of welfare is necessary for understanding the lived experience of captive chimpanzees. I propose that the inclusion of collecting more detailed positional behavior data with a focus on posture engagement and positional diversity would aid in providing a more complete understanding of the overall welfare of captive chimpanzees in a way that can direct the practices of captive management programs to improve the living conditions of these captive apes.

When seeking to alter enclosures to increase the rates of expression for desired positional behaviors within an individual chimpanzee, one must determine the effects of particular substrates on positional expression. In this study, rates of expression for positional behaviors were recorded as they relate to the use of particular substrates. However, the approach of incorporating substrates that are associated with particular types of use by the group overall may not reflect how a particular subject would tend to use the substrate. Insufficient data were collected to adequately identify the degree to which individual chimpanzees would use a given substrate if it was presented to them in conjunction with some motivation for its use. Further data would need to be collected to determine the differences in effect for particular substrates based on the individual. This is necessary as substrates may not have the intended effect if a target chimpanzee does not tend to use a substrate in the manner typical for the group as a whole. It is also the case that this type of study can only consider the potential effects of substrates present in the chimpanzees' enclosures. The substrates present, and the positional behaviors associated with their use may be separate from those that would have the most ideal positive effect on captive chimpanzees' welfare. Identifying the most beneficial substrates for producing the desired positional behaviors may require a great deal of trial and error during which different novel substrates are introduced to expand the catalogue of viable substrates present and their associated positional behaviors. Such a task could take a long time to bring to any degree of completion, particularly because subjects may not use the novel substrates to the same degree or same way over time. Further, the ways in which a particular substrate is used could vary by group, and so predictions for how a given substrate will be used may be unreliable. However, strong associations between particular substrates and positional behaviors across groups would be expected based on the similar physiology between members of this species.

The rationale for considering posture engagement in this study was derived from the difficulty of collecting objective data on locomotor behaviors to determine mobility as a correlate of overall physical and mental welfare (Hopper et al. 2022; Vereecke et al. 2011). However, even if mobility is an important factor to consider when seeking to improve welfare in captive apes, posture engagement may not be the best way to assess mobility. A detailed examination of different types of locomotor behaviors may be better able to address the question of individual mobility, as Hopper et al. (2022) suggests. Collecting such detailed data in a cost effective manner may be unfeasible, and so subjective mobility and movement fluency ratings by trained experts in captive ape welfare may be the best option for assessing this aspect of welfare (Hopper et al. 2022; Neal Webb et al. 2020).

Finally, the act of combining smaller, more detailed positional motifs into numerous different classification schemas can produce large amounts of data. Prioritizing the encouragement of particular elements of observed positional behaviors can require the placement of arbitrary or speculative value upon these elements. The inclusion of diversity scores in this thesis was intended to address this issue by providing a score that can more fully consider the totality of expressed positional behaviors while ascribing some value to the more diverse expression of these behaviors. Seeking to increase positional diversity scores among individual chimpanzees would direct efforts toward the encouragement of particular positional motifs in a way that produces an overall greater, more enriching physical experience.

5.5.3 Diversity as a Means of Assessing Welfare

Diversity scores would be made more useful if one were to address the issues plaguing positional behavior profile data collection. These include the need to collect data over longer periods of time, over larger numbers of trials per individual, and from more individuals residing in different groups with multiple demographic characteristics within different enclosure types. With these conditions met, positional diversity scores could be more adequately compared between individuals, and more accurate baselines for the typical and ideal positional diversity scores could be inferred to determine the degree to which a given individual diverges from acceptable positional diversity values. These scores, and their changes with time, would provide a means of evaluating the degree to which management practices are effectively addressing issues of limited positional diversity, while also providing means of improving conditions by considering the characteristics of the positional behavior profiles of the target group or individual. Future validation of diversity scores would be necessary for the eventual adoption of positional behavioral diversity as a welfare metric. Once validated, a particular diversity score would be advantageous as it would incorporate a complex set of attributes and experiences into one straightforward value, much like concentrations of stress hormones metabolites and immune factors do.

Despite some controversy surrounding the use of behavioral diversity as a welfare metric, individual differences in positional and substrate use diversity scores presented in this thesis support the further exploration of this approach to assessing welfare. However, conclusions about individual differences in diversity scores are dampened by the inability to compare statistical differences between Shannon diversity scores (Lyman 2008). In order for progress to be made in making behavioral diversity scores more useful and reliable metrics, refinements must be made to the categories considered in their calculations.

Among the many steps necessary to refine positional diversity metrics are the reductions of impact from confounding behaviors and positional motifs related to negative welfare states. Calculating diversity only among positional behavior expressions and among substrate type use was likely successful in preventing more disparate classes of behaviors from confounding the observed diversity scores. However, different types of positional engagements also incur varying levels of stain on and energetic expense by the body. Therefore, more efforts may be needed to create more comparable behavioral categories or ensure the appropriateness of comparing the categories present. There is also a need to address concerns of higher diversity scores being generated from the inclusion of positional motifs related to negative welfare states. The decision to include or exclude particular positional motifs may be made after further investigation into the meanings behind their expressions and the degree to which they represent undesirable states. This process would indeed take time, but constituent elements of a given positional behavior or motif would remain even after new discoveries were made for the relative value of those motifs. One could retroactively include or exclude a given behavior for the sake of comparing data taken across time as long as the basic ethogram used to collect data remained the same.

Applying behavioral diversity scores to positional behaviors presents additional issues for the appropriateness of the metric. Frequent changes in positional behavior engagement would likely lead to a greater calculated behavioral diversity score. However, frequent changes in positional behavior can also be the result of physical discomfort that prompts an animal to change postures (Bhatnager et al. 1985). This scenario involves undesired discomfort that is not conducive to the goal of positive welfare. One would not want to use perceived behavioral diversity to justify practices that chiefly promote physical discomfort.

Diversity in positional behavior and substrate use profiles can not only describe the states of subjects, but can offer guidance as to where efforts should be placed and what actions could be taken to improve welfare. It is important to note that any positional profiles, substrate profiles, and diversity scores require interpretation, just like any other welfare metric. While it may be difficult to make absolute determinations about the directions to take captive management practices based on positional behavior and substrate use data, these can be used as tools to inform the judgement of animal caretakers when making changes. With the deployment of human empathy in concert with positional behavior data, the refinement of this metric may be accelerated.

If further refinement of positional behavioral diversity metrics are needed for this measure to accurately coincide with welfare, one can still make use of the same prerequisite data used to calculate behavioral diversity and apply it toward other purposes. In identifying postures indicative of poor physical health for comparative analysis of particular positional behavior engagement, one could exclude these positional categories from use in calculating behavioral diversity metrics. The usefulness of these data apart from calculating positional behavioral diversity provide an opportunity to validate welfare assessments that are based on both behavioral diversity and expression of positive versus negative positional behaviors with more established welfare measurements.

Positional diversity scores could provide more complete insights into the observable attributes of the physical states of chimpanzees when compared to the degree to which stress hormone analysis can take into account the complexities of internal emotional states (Otovic and Hutchinson 2014). However, diversity scores require a greater degree of subjectivity in generating the classification schemas that produce the ultimate diversity value. Stress hormone concentration analysis also has the advantage of generating snapshots of welfare states during the timeframe defined by the methods of sample collection (Whitham et al. 2020). Generating positional diversity scores requires greater time investments, but may be more cost-effective if similar behavioral data are already being collected. Given that medical treatment is a large part of efforts to sustain wellbeing in captive animals, the data collected to generate positional diversity scores would also provide benefit for monitoring general physical health in a way that also benefits the medical approach to addressing welfare concerns. If medical benefits are associated with attention paid to collecting regular quantitative data on limb use, this same data could provide additional insights into the positional tendencies of individuals via generating diversity scores in a way that does not interfere with other welfare monitoring practices. Using collected positional data in ways that improve medical treatment outcomes would allow for the aggregation of data that is needed to refine the behavioral diversity metric without allocating undo resources toward an unrefined welfare metric.

Chapter 6: Conclusion

The expressions of positional behaviors by captive animals are essential, and often overlooked, aspects of their overall physical and emotional well-beings. While some recent chimpanzee welfare studies have demonstrated the usefulness of considering positional behavioral expressions when assessing welfare, the surface of this approach to promoting primate welfare has only been scratched. The development of this approach is hindered by the difficulties involved in positional data collection, identifying positional correlates of positive and negative welfare, and effectively enacting practices to promote welfare as it relates to positional behavioral expression.

This thesis provides preliminary evidence of the potential to achieve further advancements in the positional behavior approach to monitoring and promoting captive primate welfare. By utilizing an ethogram that records the engagements for each limb and the axial portion of the body, one can generate large numbers of possible postures that the chimpanzees can embody. Numerous ways of combining positional elements into behavioral classification schemas can provide useful, even if overwhelming, detail regarding the distinct, individual patterns of positional behavior.

Generating positional behavior profiles and calculating the Shannon diversity index under a given positional behavior classification schema could provide several benefits to the practice of monitoring health and welfare among captive individuals. One could identify subtle evidence of present injuries, or the likelihood of such ailments befalling a chimpanzee in the future due to lack of use. Positional behaviors may also serve outward functions that could signal particular emotional states to an observer. Diversity indices provide a concrete value that may correlate with overall welfare in captive individuals. However, in order for material benefits to manifest from detailed positional behavior data collection, a subject's positional diversity score and rates of expressing particular positional behaviors and motifs must be validated by comparison to established welfare metrics, known medical status, and the social contexts present while engaging a given positional mode.

The failure of the novel climbing aid to increase climbing behaviors and platform structure use suggests that an alternative approach be taken to the design of structural modifications, their manner of implementation, assessing their effectiveness, or a combination of these. In part due to the short-term nature of this study, conclusions cannot be made as to the long-term or potential value of the novel climbing aid. Alternative approaches to implementing future structural modifications could be informed in part by the substrate use profiles of the enclosure's resident group members.

Substrate use profiles and diversity scores could be monitored in part to infer the internal states of chimpanzees as they relate to the willingness for an individual to interact with particular elements of their enclosure. Understanding individual substrate use tendencies can help to inform enclosure designs and modifications such that the types of features that chimpanzees prefer to use are more prevalent or located in key enclosure areas such that resident chimpanzees can be encouraged to make use of beneficial enclosure areas. The relationship between particular substrates and positional behavior expressions may be used to promote the engagement of a chimpanzee in positional behaviors thought to be beneficial to their wellbeing. Simultaneously considering positional behavior and substrate use can provide not only an assessment of the state of a subject, but can also produce a roadmap for beneficial ways that an enclosure can be altered to the benefit of captive residents.

Despite the need for further refinement of data collection and analysis practices relating to enacting a positional behavior approach to welfare, the urgency of promoting welfare for animals currently living in captivity should motivate this refinement process. If detailed positional behavior and substrate use data could be added to the list of viable welfare measurements, a more holistic view of welfare could be achieved, thus enabling captive management programs to take into greater consideration the role of captive primates' physical environments and their positions therein to create conditions more favorable to the captive animals.

References

Abou-Ismail, U. A., Burman, O. H. P., Nicol, C. J., & Mendl, M. (2010). The effects of enhancing cage complexity on the behaviour and welfare of laboratory rats. *Behavioural Processes*, *85*(2), 172–180. https://doi.org/10.1016/j.beproc.2010.07.002

Almécija, S., Hammond, A. S., Thompson, N. E., Pugh, K. D., Moyà-Solà, S., & Alba, D. M. (2021). Fossil apes and human evolution. *Science*, *372*(6542), eabb4363. https://doi.org/10.1126/science.abb4363

Anderson, J. R. (2018). Chimpanzees and death. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1754), 20170257. https://doi.org/10.1098/rstb.2017.0257

Anestis, S. F. (2009). Urinary cortisol responses to unusual events in captive chimpanzees (*Pan troglodytes*). *Stress*, *12*(1), 49–57. https://doi.org/10.1080/10253890802041308

Ang, M. Y. L., Shender, M. A., & Ross, S. R. (2017). Assessment of behavior and space use before and after forelimb amputation in a zoo-housed chimpanzee (*Pan troglodytes*): Behavioral Effects of Forelimb Amputation in a Chimpanzee. *Zoo Biology*, *36*(1), 5–10. https://doi.org/10.1002/zoo.21345

Appleby, M. C. (1997). Life in a variable world: Behaviour, welfare and environmental design. *Applied Animal Behaviour Science*, *54*(1), 1–19. https://doi.org/10.1016/S0168-1591(96)01197-5

Archie, E. A. (2013). Wound healing in the wild: Stress, sociality, and energetic costs affect wound healing in natural populations. *Parasite Immunology*, n/a-n/a. https://doi.org/10.1111/pim.12048

Ardila, A. (2008). On the evolutionary origins of executive functions. *Brain and Cognition*, *68*(1), 92–99. https://doi.org/10.1016/j.bandc.2008.03.003

AZA Ape TAG. (2010). *Chimpanzee (Pan troglodytes) care manual.*

Bak, A., Tsiami, A., & Greene, C. (2017). Methods of Assessment of Hydration Status and their Usefulness in Detecting Dehydration in the Elderly. *Current Research in Nutrition and Food Science Journal*, *5*(2), 43–54. https://doi.org/10.12944/CRNFSJ.5.2.01

Baker, K. C., & Aureli, F. (1996). The neighbor effect: Other groups influence intragroup agonistic behavior in captive chimpanzees. *American Journal of Primatology*, *40*(3), 283–291. https://doi.org/10.1002/(SICI)1098-2345(1996)40:3<283::AID-AJP5>3.0.CO;2-U

Baker, K. C., & Aureli, F. (1997). Behavioural Indicators of Anxiety: An Empirical Test in Chimpanzees. *Behaviour*, *134*(13–14), 1031–1050. https://doi.org/10.1163/156853997X00386

Barss, P., Dakulala, P., & Doolan, M. (1984). Falls from trees and tree associated injuries in rural Melanesians. *BMJ*, *289*(6460), 1717–1720. https://doi.org/10.1136/bmj.289.6460.1717

Bassett, L., & Buchanan-Smith, H. M. (2007). Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science*, *102*(3–4), 223–245. https://doi.org/10.1016/j.applanim.2006.05.029

Bateson, M. (2016). Cumulative stress in research animals: Telomere attrition as a biomarker in a welfare context? *BioEssays*, *38*(2), 201–212. https://doi.org/10.1002/bies.201500127

Bateson, M., & Nettle, D. (2015). Development of a cognitive bias methodology for measuring low mood in chimpanzees. *PeerJ*, *3*, e998. https://doi.org/10.7717/peerj.998

Bateson, M., & Poirier, C. (2019). Can biomarkers of biological age be used to assess cumulative lifetime experience? *Animal Welfare*, *28*(1), 41–56. https://doi.org/10.7120/09627286.28.1.041

Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*, *5*(1), 180214. https://doi.org/10.1038/sdata.2018.214

Behringer, V., & Deschner, T. (2017). Non-invasive monitoring of physiological markers in primates. *Hormones and Behavior*, *91*, 3–18. https://doi.org/10.1016/j.yhbeh.2017.02.001

Behringer, V., Stevens, J. M. G., Hohmann, G., Möstl, E., Selzer, D., & Deschner, T. (2014). Testing the Effect of Medical Positive Reinforcement Training on Salivary Cortisol Levels in Bonobos and Orangutans. *PLoS ONE*, *9*(9), e108664. https://doi.org/10.1371/journal.pone.0108664

Beisner, B. A., Hannibal, D. L., Vandeleest, J. J., & McCowan, B. (2023). Sociality, Health, and Welfare in Nonhuman Primates. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare* (pp. 413–443). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_18

Beisner, B. A., & Isbell, L. A. (2008). Ground substrate affects activity budgets and hair loss in outdoor captive groups of rhesus macaques (*Macaca mulatta*). *American Journal of Primatology*, *70*(12), 1160–1168. https://doi.org/10.1002/ajp.20615

Berghänel, A., Schülke, O., & Ostner, J. (2015). Locomotor play drives motor skill acquisition at the expense of growth: A life history trade-off. *Science Advances*, *1*(7), e1500451. https://doi.org/10.1126/sciadv.1500451

Bethell, E., Holmes, A., MacLarnon, A., & Semple, S. (2012). Cognitive bias in a non-human primate: Husbandry procedures influence cognitive indicators of psychological well-being in captive rhesus macaques. *Animal Welfare*, *21*(2), 185–195. https://doi.org/10.7120/09627286.21.2.185

Bettinger, T., Wallis, J., & Carter, T. (1994). Spatial selection in captive adult female chimpanzees. *Zoo Biology*, *13*(2), 167–176. https://doi.org/10.1002/zoo.1430130208

Bezanson, M. (2017). Primate Positional Behavior Development and Evolution. *Annual Review of Anthropology*, *46*(1), 279–298. https://doi.org/10.1146/annurev-anthro-102116-041503

Bhatnager, V., Drury, C. G., & Schiro, S. G. (1985). Posture, Postural Discomfort, and Performance. *Human Factors: The Journal of the Human Factors and Ergonomics Society*, *27*(2), 189–199. https://doi.org/10.1177/001872088502700206

Bidner, L. R., Matsumoto-Oda, A., & Isbell, L. A. (2018). The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. *American Journal of Primatology*, *80*(12). https://doi.org/10.1002/ajp.22932

Birkett, L. P., & Newton-Fisher, N. E. (2011). How Abnormal Is the Behaviour of Captive, Zoo-Living Chimpanzees? *PLoS ONE*, *6*(6), e20101. https://doi.org/10.1371/journal.pone.0020101

Bismark, M. (2010). Proboscis Monkey (Nasalis larvatus): Bio-ecology and Conservation. In S. Gursky & J. Supriatna (Eds.), *Indonesian Primates* (pp. 217–233). Springer New York. https://doi.org/10.1007/978-1-4419-1560-3_12

Bloom, T., & Friedman, H. (2013). Classifying dogs' (Canis familiaris) facial expressions from photographs. *Behavioural Processes*, *96*, 1–10. https://doi.org/10.1016/j.beproc.2013.02.010

Boerema, S. T., van Velsen, L., Vollenbroek-Hutten, M. M. R., & Hermens, H. J. (2017). Value-based design for the elderly: An application in the field of mobility aids. *Assistive Technology*, *29*(2), 76–84. https://doi.org/10.1080/10400435.2016.1208303

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press.

Bonnichsen, M., Dragsted, N., & Hansen, A. (2005). The welfare impact of gavaging laboratory rats. *Animal Welfare*, *14*(3), 223–227. https://doi.org/10.1017/S0962728600029389

Bonnie, K. E., & de Waal, F. B. M. (2006). Affiliation promotes the transmission of a social custom: Handclasp grooming among captive chimpanzees. *Primates*, *47*(1), 27–34. https://doi.org/10.1007/s10329-005-0141-0

Boyer Ontl, K., & Pruetz, J. D. (2020). Mothers Frequent Caves: Lactation Affects Chimpanzee (Pan troglodytes verus) Cave Use in Southeastern Senegal. *International Journal of Primatology*, *41*(6), 916–935. https://doi.org/10.1007/s10764-020-00165-4

Bradshaw, G. A., Capaldo, T., Lindner, L., & Grow, G. (2008). Building an Inner Sanctuary: Complex PTSD in Chimpanzees. *Journal of Trauma & Dissociation*, *9*(1), 9–34. https://doi.org/10.1080/15299730802073619

Brando, S., & Coe, J. (2022). Confronting Back-of-House Traditions: Primates as a Case Study. *Journal of Zoological and Botanical Gardens*, *3*(3), 366–397. https://doi.org/10.3390/jzbg3030029

Britt, S., Cowlard, K., Baker, K., & Plowman, A. (2015). Aggression and self-directed behaviour of captive lemurs (Lemur catta, Varecia variegata, V. rubra and Eulemur coronatus) is reduced by feeding fruit-free diets. *Journal of Zoo and Aquarium Research*, *3*(2), 52–58. https://doi.org/10.19227/jzar.v3i2.119

Browning, H. (2020). The Natural Behavior Debate: Two Conceptions of Animal Welfare. *Journal of Applied Animal Welfare Science*, *23*(3), 325–337. https://doi.org/10.1080/10888705.2019.1672552

Browning, H., & Veit, W. (2021). Freedom and Animal Welfare. *Animals*, *11*(4), 1148. https://doi.org/10.3390/ani11041148

Brownson, R. C., Hoehner, C. M., Day, K., Forsyth, A., & Sallis, J. F. (2009). Measuring the Built Environment for Physical Activity. *American Journal of Preventive Medicine*, *36*(4), S99-S123.e12. https://doi.org/10.1016/j.amepre.2009.01.005

Burghardt, G. M. (2014). A Brief Glimpse at the Long Evolutionary History of Play. *Animal Behavior and Cognition*, *2*(2), 90. https://doi.org/10.12966/abc.05.01.2014

Cairo-Evans, A., Wierzal, N. K., Wark, J. D., & Cronin, K. A. (2022). Do zoo-housed primates retreat from crowds? A simple study of five primate species. *American Journal of Primatology*, *84*(10). https://doi.org/10.1002/ajp.23386

Cannon, C. H., & Leighton, M. (1994). Comparative locomotor ecology of gibbons and macaques: Selection of canopy elements for crossing gaps. *American Journal of Physical Anthropology*, *93*(4), 505–524. https://doi.org/10.1002/ajpa.1330930409

Capitanio, J. P., Vandeleest, J., & Hannibal, D. L. (2023). Physiological Measures of Welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare* (pp. 231–254). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_10

Caravaggi, A., Plowman, A., Wright, D. J., & Bishop, C. M. (2018). The composition of captive ruffed lemur (Varecia spp.) diets in UK zoological collections, with reference to the problems of obesity and iron storage disease. *Journal of Zoo and Aquarium Research*, *6*(2), 41–49. https://doi.org/10.19227/jzar.v6i2.301

Carrier, D. R. (2007). The short legs of great apes: evidence for aggressive behavior in australopiths. *Evolution*, *61*(3), 596–605. https://doi.org/10.1111/j.1558-5646.2007.00061.x

Cartmill, M. (1974). Pads and Claws in Arboreal Locomotion. In *Primate Locomotion* (pp. 45–83). Elsevier. https://doi.org/10.1016/B978-0-12-384050-9.50007-6

Cartmill, M. (1979). The volar skin of primates: Its frictional characteristics and their functional significance. *American Journal of Physical Anthropology*, *50*(4), 497–509. https://doi.org/10.1002/ajpa.1330500402

Casado, A., Avià, Y., Llorente, M., Riba, D., Pastor, J. F., & Potau, J. M. (2021). Effects of Captivity on the Morphology of the Insertion Sites of the Palmar Radiocarpal Ligaments in Hominoid Primates. *Animals*, *11*(7), 1856. https://doi.org/10.3390/ani11071856

Caws, C., Wehnelt, S., & Aureli, F. (2008). The effect of a new vertical structure in mitigating aggressive behaviour in a large group of chimpanzees *(Pan troglodytes)*. *Animal Welfare*, *17*(2), 149–154. https://doi.org/10.1017/S0962728600027652

Celli, M. L., Tomonaga, M., Udono, T., Teramoto, M., & Nagano, K. (2003). Tool use task as environmental enrichment for captive chimpanzees. *Applied Animal Behaviour Science*, *81*(2), 171–182. https://doi.org/10.1016/S0168-1591(02)00257-5

ChimpHaven.org. (n.d.). About Us. retrieved from https://chimphaven.org/about-us/

Cheyne, S. M. (2011). Gibbon Locomotion Research in the Field: Problems, Possibilities, and Benefits for Conservation. In K. D'Août & E. E. Vereecke (Eds.), *Primate Locomotion* (pp. 201–213). Springer New York. https://doi.org/10.1007/978-1-4419-1420-0_11

Clark, F. E. (2011). Space to choose: Network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, *73*(8), 748–757. https://doi.org/10.1002/ajp.20903

Clark, J. D., Rager, D. R., & Calpin, J. P. (1997). Animal well-being. II. Stress and distress. *Laboratory Animal Science*, *47*(6), 571–579.

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*(1–2), 1–10. https://doi.org/10.1016/j.applanim.2011.03.002

Clayton, J. B., Vangay, P., Huang, H., Ward, T., Hillmann, B. M., Al-Ghalith, G. A., Travis, D. A., Long, H. T., Tuan, B. V., Minh, V. V., Cabana, F., Nadler, T., Toddes, B., Murphy, T., Glander, K. E., Johnson, T. J., & Knights, D. (2016). Captivity humanizes the primate microbiome. *Proceedings of the National Academy of Sciences*, *113*(37), 10376–10381. https://doi.org/10.1073/pnas.1521835113

Clubb, R., & Mason, G. (2003). Captivity effects on wide-ranging carnivores. *Nature*, *425*(6957), 473–474. https://doi.org/10.1038/425473a

Clubb, R., Rowcliffe, M., Lee, P., Mar, K. U., Moss, C., & Mason, G. J. (2008). Compromised Survivorship in Zoo Elephants. *Science*, *322*(5908), 1649–1649. https://doi.org/10.1126/science.1164298

Cole, M. F., Cantwell, A., Rukundo, J., Ajarova, L., Fernandez-Navarro, S., Atencia, R., & Rosati, A. G. (2020). Healthy cardiovascular biomarkers across the lifespan in wild-born chimpanzees (*Pan troglodytes*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1811), 20190609. https://doi.org/10.1098/rstb.2019.0609

Coleman, K., & Pierre, P. J. (2014). Assessing Anxiety in Nonhuman Primates. *ILAR Journal*, *55*(2), 333–346. https://doi.org/10.1093/ilar/ilu019

Couturier, C., Bortolamiol, S., Ortmann, S., Okimat, J.-P., Asalu, E., & Krief, S. (2022). All-You-Can-Eat: Influence of Proximity to Maize Gardens on the Wild Diet and the Forest Activities of the Sebitoli Chimpanzee Community in Kibale National Park. *Animals*, *12*(7), 806. https://doi.org/10.3390/ani12070806

Cronin, K., & Ross, S. (2019). Technical contribution: A cautionary note on the use of behavioural diversity (H-Index) in animal welfare science. *Animal Welfare*, *28*(2), 157–164. https://doi.org/10.7120/09627286.28.2.157

D’Anci, K. E., Constant, F., & Rosenberg, I. H. (2006). Hydration and Cognitive Function in Children. *Nutrition Reviews*, *64*(10), 457–464. https://doi.org/10.1111/j.1753-4887.2006.tb00176.x

Dawkins, M. (2006). A user’s guide to animal welfare science. *Trends in Ecology & Evolution*, *21*(2), 77–82. https://doi.org/10.1016/j.tree.2005.10.017

de Vries, N. M., van Ravensberg, C. D., Hobbelen, J. S. M., Olde Rikkert, M. G. M., Staal, J. B., & Nijhuis-van der Sanden, M. W. G. (2012). Effects of physical exercise therapy on mobility, physical functioning, physical activity and quality of life in community-dwelling older adults with impaired mobility, physical disability and/or multi-morbidity: A meta-analysis. *Ageing Research Reviews*, *11*(1), 136–149. https://doi.org/10.1016/j.arr.2011.11.002

D’Eath, R. B., Tolkamp, B. J., Kyriazakis, I., & Lawrence, A. B. (2009). ‘Freedom from hunger’ and preventing obesity: The animal welfare implications of reducing food quantity or quality. *Animal Behaviour*, *77*(2), 275–288. https://doi.org/10.1016/j.anbehav.2008.10.028

Demes, B., Thompson, N. E., O’Neill, M. C., & Umberger, B. R. (2015). Center of mass mechanics of chimpanzee bipedal walking: Center of Mass Mechanics in Chimpanzee Bipedalism. *American Journal of Physical Anthropology*, *156*(3), 422–433. https://doi.org/10.1002/ajpa.22667

Demuru, E., Pellegrino, F., Dediu, D., & Levréro, F. (2020). Foraging postures are a potential communicativesignal in female bonobos. *Scientific Reports*, *10*(1), 15431. https://doi.org/10.1038/s41598-020-72451-3

Descovich, K. (2017). Facial expression: An under-utilised tool for the assessment of welfare in mammals. *ALTEX*. https://doi.org/10.14573/altex.1607161

Doran, D. M. (1993). Sex differences in adult chimpanzee positional behavior: The influence of body size on locomotion and posture. *American Journal of Physical Anthropology*, *91*(1), 99–115. https://doi.org/10.1002/ajpa.1330910107

Dorey, N. R., Rosales-Ruiz, J., Smith, R., Lovelace, B., & Roane, H. (2009). FUNCTIONAL ANALYSIS AND TREATMENT OF SELF-INJURY IN A CAPTIVE OLIVE BABOON. *Journal of Applied Behavior Analysis*, *42*(4), 785–794. https://doi.org/10.1901/jaba.2009.42-785

Doyle, L. A., Baker, K. C., & Cox, L. D. (2008). Physiological and behavioral effects of social introduction on adult male rhesus macaques. *American Journal of Primatology*, *70*(6), 542–550. https://doi.org/10.1002/ajp.20526

Du Clos, T. W. (2000). Function of C-reactive protein. *Annals of Medicine*, *32*(4), 274–278. https://doi.org/10.3109/07853890009011772

Duncan, L. M., D'Egidio Kotze, C., & Pillay, N. (2022). Long-Term Spatial Restriction Generates Deferred Limited Space Use in a Zoo-Housed Chimpanzee Group. *Animals*, *12*(17), 2207. https://doi.org/10.3390/ani12172207

Duncan, L. M., Jones, M. A., van Lierop, M., & Pillay, N. (2013). Chimpanzees use multiple strategies to limit aggression and stress during spatial density changes. *Applied Animal Behaviour Science*, *147*(1–2), 159–171. https://doi.org/10.1016/j.applanim.2013.06.001

Earl, S. C., Hopper, L. M., & Ross, S. R. (2020). Same Space, Different Species: The Influence of Exhibit Design on the Expression of Zoo-Housed Apes' Species-Typical Retiring Behaviors. *Animals*, *10*(5), 836. https://doi.org/10.3390/ani10050836

Ely, J. J., Zavaskis, T., & Lammey, M. L. (2013). Hypertension Increases With Aging and Obesity in Chimpanzees (Pan troglodytes): Hypertension in Chimpanzees. *Zoo Biology*, *32*(1), 79–87. https://doi.org/10.1002/zoo.21044

Enigk, D. K., Thompson, M. E., Machanda, Z. P., Wrangham, R. W., & Muller, M. N. (2020). Competitive ability determines coalition participation and partner selection during maturation in wild male chimpanzees (Pan troglodytes schweinfurthii). *Behavioral Ecology and Sociobiology*, *74*(7), 89. https://doi.org/10.1007/s00265-020-02872-7

Fernandez, E. (2022). Training as enrichment: A critical review. *Animal Welfare*, *31*(1), 1–12. https://doi.org/10.7120/09627286.31.1.001

Ferry-Graham, L. A. (2002). Using Functional Morphology to Examine the Ecology and Evolution of Specialization. *Integrative and Comparative Biology*, *42*(2), 265–277. https://doi.org/10.1093/icb/42.2.265

Finkel, B. (2022). *Activity, but not physiological condition, declines in aging male chimpanzees (Pan troglodytes)*.

Franks, B. (2019). What do animals want? *Animal Welfare*, *28*(1), 1–10. https://doi.org/10.7120/09627286.28.1.001

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences*, *105*(25), 8557–8562. https://doi.org/10.1073/pnas.0804141105

Friesen, S. E., Knigge, R. P., Jashashvili, T., Harcourt-Smith, W. E. H., Schoeninger, M. J., & Tocheri, M. W. (2022). Shape variation in the talus and medial cuneiform of chimpanzees and bonobos. *American Journal of Biological Anthropology*, ajpa.24571. https://doi.org/10.1002/ajpa.24571

Fultz, A., Yanagi, A., Breaux, S., Beaupre, L., & Naitove, N. (2023). How Sanctuary Chimpanzees (Pan troglodytes) Use Space after Being Introduced to a Large Outdoor Habitat. *Animals*, *13*(6), 961. https://doi.org/10.3390/ani13060961

Funkhouser, J. A., Mayhew, J. A., & Mulcahy, J. B. (2018). Social network and dominance hierarchy analyses at Chimpanzee Sanctuary Northwest. *PLOS ONE*, *13*(2), e0191898. https://doi.org/10.1371/journal.pone.0191898

Futuyma, D. J., & Moreno, G. (1988). THE EVOLUTION OF ECOLOGICAL SPECIALIZATION. *Annual Review of Ecology and Systematics*, *19*(1), 207–233. https://doi.org/10.1146/annurev.es.19.110188.001231

Gaengler, H., & Clum, N. (2015). Investigating the impact of large carcass feeding on the behavior of captive Andean condors (*Vultur gryphus*) and its perception by zoo visitors: Carcass Feeding for Captive Vultures. *Zoo Biology*, *34*(2), 118–129. https://doi.org/10.1002/zoo.21202

Garner, J. P. (2005). Stereotypies and Other Abnormal Repetitive Behaviors: Potential Impact on Validity, Reliability, and Replicability of Scientific Outcomes. *ILAR Journal*, *46*(2), 106–117. https://doi.org/10.1093/ilar.46.2.106

Garner, J. P. (2006). Perseveration and stereotypy—Systems-level insights from clinical psychology. In G. Mason & J. Rushen (Eds.), *Stereotypic animal behaviour: Fundamentals* *and applications to welfare* (2nd ed., pp. 121–152). CABI. https://doi.org/10.1079/9780851990040.0121

Gartner, M. C., & Weiss, A. (2018). Studying primate personality in zoos: Implications for the management, welfare and conservation of great apes. *International Zoo Yearbook*, *52*(1), 79–91. https://doi.org/10.1111/izy.12187

Graham, K. E., & Hobaiter, C. (2023). Towards a great ape dictionary: Inexperienced humans understand common nonhuman ape gestures. *PLOS Biology*, *21*(1), e3001939. https://doi.org/10.1371/journal.pbio.3001939

Graham, M., & Socha, J. J. (2020). Going the distance: The biomechanics of gap-crossing behaviors. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *333*(1), 60–73. https://doi.org/10.1002/jez.2266

Granatosky, M. C. (2018). A Review of locomotor diversity in mammals with analyses exploring the influence of substrate use, body mass and intermembral index in primates. *Journal of Zoology*, *306*(4), 207–216. https://doi.org/10.1111/jzo.12608

Granatosky, M. C. (2020). Primate Locomotion. In J. Vonk & T. Shackelford (Eds.), *Encyclopedia of Animal Cognition and Behavior* (pp. 1–7). Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_1833-1

Granatosky, M. C., Schmitt, D., & Hanna, J. (2018). Comparison of spatiotemporal gait characteristics between vertical climbing and horizontal walking in primates. *Journal of Experimental Biology*, jeb.185702. https://doi.org/10.1242/jeb.185702

Green, S. J., Boruff, B. J., Niyigaba, P., Ndikubwimana, I., & Grueter, C. C. (2020). Chimpanzee ranging responses to fruit availability in a high-elevation environment. *American Journal of Primatology*, *82*(5). https://doi.org/10.1002/ajp.23119

Hall, K., Bryant, J., Staley, M., Whitham, J., & Miller, L. (2021). Behavioural diversity as a potential welfare indicator for professionally managed chimpanzees (Pan troglodytes): Exploring variations in calculating diversity using species-specific behaviours. *Animal Welfare*, *30*(4), 381–392. https://doi.org/10.7120/09627286.30.4.002

Hanna, J. B., Granatosky, M. C., Rana, P., & Schmitt, D. (2017). The evolution of vertical climbing in primates: Evidence from reaction forces. *Journal of Experimental Biology*, jeb.157628. https://doi.org/10.1242/jeb.157628

Hanna, J. B., & Schmitt, D. (2011). Locomotor energetics in primates: Gait mechanics and their relationship to the energetics of vertical and horizontal locomotion. *American Journal of Physical Anthropology*, *145*(1), 43–54. https://doi.org/10.1002/ajpa.21465

Hänsel, A., Hong, S., Cámara, R. J. A., & von Känel, R. (2010). Inflammation as a psychophysiological biomarker in chronic psychosocial stress. *Neuroscience & Biobehavioral Reviews*, *35*(1), 115–121. https://doi.org/10.1016/j.neubiorev.2009.12.012

Hanson, N. K. I. H. (2016). C*ognitive and locomotor strategies of arboreal locomotion in non-human apes and humans* [PhD Thesis]. University of Birmingham.

Hau, J., & Schapiro, S. J. (2007). The welfare of non-human primates. In E. Kaliste (Ed.), *The Welfare of Laboratory Animals* (Vol. 2, pp. 291–314). Springer Netherlands. https://doi.org/10.1007/978-1-4020-2271-5_13

Heintz, M. R., Santymire, R. M., Parr, L. A., & Lonsdorf, E. V. (2011). Validation of a cortisol enzyme immunoassay and characterization of salivary cortisol circadian rhythm in chimpanzees (Pan troglodytes). *American Journal of Primatology*, *73*(9), 903–908. https://doi.org/10.1002/ajp.20960

Heistermann, M. (2010). Non-invasive monitoring of endocrine status in laboratory primates: Methods, guidelines and applications. *Advances in Science and Research*, *5*(1), 1–9. https://doi.org/10.5194/asr-5-1-2010

Heistermann, M., & Higham, J. P. (2015). Urinary neopterin, a non-invasive marker of mammalian cellular immune activation, is highly stable under field conditions. *Scientific Reports*, *5*(1), 16308. https://doi.org/10.1038/srep16308

Held, S. D. E., & Špinka, M. (2011). Animal play and animal welfare. *Animal Behaviour*, *81*(5), 891–899. https://doi.org/10.1016/j.anbehav.2011.01.007

Hobaiter, C., & Byrne, R. W. (2014). The Meanings of Chimpanzee Gestures. *Current Biology*, *24*(14), 1596–1600. https://doi.org/10.1016/j.cub.2014.05.066

Hoehfurtner, T., Wilkinson, A., Nagabaskaran, G., & Burman, O. H. P. (2021). Does the provision of environmental enrichment affect the behaviour and welfare of captive snakes? *Applied Animal Behaviour Science*, *239*, 105324. https://doi.org/10.1016/j.applanim.2021.105324

Holowka, N. B., O'Neill, M. C., Thompson, N. E., & Demes, B. (2017). Chimpanzee ankle and foot joint kinematics: Arboreal versus terrestrial locomotion. *American Journal of Physical Anthropology*, *164*(1), 131–147. https://doi.org/10.1002/ajpa.23262

Honess, P. E., & Marin, C. M. (2006). Enrichment and aggression in primates. *Neuroscience & Biobehavioral Reviews*, *30*(3), 413–436. https://doi.org/10.1016/j.neubiorev.2005.05.002

Hopper, L. M., Lake, B. R., Leinwand, J. G., Fultz, A., & Ross, S. R. (2022). Assessing chimpanzees' fluency of movement: Applications for monitoring health and welfare. *Applied Animal Behaviour Science*, *250*, 105612. https://doi.org/10.1016/j.applanim.2022.105612

Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal Cognition*, *17*(4), 835–847. https://doi.org/10.1007/s10071-013-0715-y

Houle, A., Chapman, C. A., & Vickery, W. L. (2010). Intratree vertical variation of fruit density and the nature of contest competition in frugivores. *Behavioral Ecology and Sociobiology*, *64*(3), 429–441. https://doi.org/10.1007/s00265-009-0859-6

Houle, A., & Wrangham, R. W. (2021). Contest competition for fruit and space among wild chimpanzees in relation to the vertical stratification of metabolizable energy. *Animal Behaviour*, *175*, 231–246. https://doi.org/10.1016/j.anbehav.2021.03.003

Hunt, K. D. (1991). Mechanical implications of chimpanzee positional behavior. *American Journal of Physical Anthropology*, *86*(4), 521–536. https://doi.org/10.1002/ajpa.1330860408

Hunt, K. D. (1992). Positional behavior ofPan troglodytes in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *American Journal of Physical Anthropology*, *87*(1), 83–105. https://doi.org/10.1002/ajpa.1330870108

Hunt, K. D. (2016). Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *Journal of Anatomy*, *228*(4), 630–685. https://doi.org/10.1111/joa.12454

Hunt, K. D., Cant, J. G. H., Gebo, D. L., Rose, M. D., Walker, S. E., & Youlatos, D. (1996). Standardized descriptions of primate locomotor and postural modes. *Primates*, *37*(4), 363–387. https://doi.org/10.1007/BF02381373

Huseynov, A., Ponce de León, M. S., & Zollikofer, C. P. E. (2017). development of modular organization in the chimpanzee pelvis: modular organization in the chimpanzee pelvis. *The Anatomical Record*, *300*(4), 675–686. https://doi.org/10.1002/ar.23548

Inoue, N., & Shimada, M. (2020). Comparisons of Activity Budgets, Interactions, and Social Structures in Captive and Wild Chimpanzees (Pan troglodytes). *Animals*, *10*(6), 1063. https://doi.org/10.3390/ani10061063

Isbell, L. A., Pruetz, J. D., Lewis, M., & Young, T. P. (1998). Locomotor activity differences between sympatric patas monkeys (Erythrocebus patas) and vervet monkeys (Cercopithecus aethiops): Implications for the evolution of long hindlimb length inHomo. *American Journal of Physical Anthropology*, *105*(2), 199–207. https://doi.org/10.1002/(SICI)1096-8644(199802)105:2<199::AID-AJPA7>3.0.CO;2-Q

Isler, K. (2005). 3D-kinematics of vertical climbing in hominoids. *American Journal of Physical Anthropology*, *126*(1), 66–81. https://doi.org/10.1002/ajpa.10419

Jacobson, S. L., Freeman, H. D., Santymire, R. M., & Ross, S. R. (2017). Atypical experiences of captive chimpanzees (*Pan troglodytes*) are associated with higher hair cortisol concentrations as adults. *Royal Society Open Science*, *4*(12), 170932. https://doi.org/10.1098/rsos.170932

Jamtvedt, G., Dahm, K. T., Christie, A., Moe, R. H., Haavardsholm, E., Holm, I., & Hagen, K. B. (2008). Physical Therapy Interventions for Patients With Osteoarthritis of the Knee: An Overview of Systematic Reviews. *Physical Therapy*, *88*(1), 123–136. https://doi.org/10.2522/ptj.20070043

Janson, C. H. (2007). Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition*, *10*(3), 341–356. https://doi.org/10.1007/s10071-007-0079-2

Jensvold, M. L. A., Sanz, C. M., Fouts, R. S., & Fouts, D. H. (2001). Effect of Enclosure Size and Complexity on the Behaviors of Captive Chimpanzees (Pan troglodytes). *Journal of Applied Animal Welfare Science*, *4*(1), 53–69. https://doi.org/10.1207/S15327604JAWS0401_3

Jesse G. Leinwand, Jill A. Moyse, Lydia M. Hopper, Maureen Leahy, & Ross, S. R. (2021). The Use of biofloors in great ape zoo exhibits. *Journal of Zoo and Aquarium Research*, *9*(1), 41–48. https://doi.org/10.19227/jzar.v9i1.544

Judge, P. G., Griffaton, N. S., & Fincke, A. M. (2006). Conflict management by hamadryas baboons (Papio hamadryas hamadryas) during crowding: A tension-reduction strategy. *American Journal of Primatology*, *68*(10), 993–1006. https://doi.org/10.1002/ajp.20290

Junge, R. E., Gannon, F. H., Porton, I., McAlister, W., & Whyte, M. (2000). management and prevention of vitamin d deficiency rickets in captive-born juvenile chimpanzees (pan troglodytes). *Journal of Zoo and Wildlife Medicine*, *31*(3), 361–369. https://doi.org/10.1638/1042-7260(2000)031[0361:MAPOVD]2.0.CO;2

Jurado, M. B., & Rosselli, M. (2007). The Elusive Nature of Executive Functions: A Review of our Current Understanding. *Neuropsychology Review*, *17*(3), 213–233. https://doi.org/10.1007/s11065-007-9040-z

Kemp, C. (2023). Enrichment. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare* (pp. 463–500). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_20

Kivell, T. L., & Schmitt, D. (2009). Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proceedings of the National Academy of Sciences*, *106*(34), 14241–14246. https://doi.org/10.1073/pnas.0901280106

Kosheleff, V. P., & Anderson, C. N. K. (2009). Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, *139*(2), 172–181. https://doi.org/10.1002/ajpa.20970

Koski, S. E., Koops, K., & Sterck, E. H. M. (2007). Reconciliation, relationship quality, and postconflict anxiety: Testing the integrated hypothesis in captive chimpanzees. *American Journal of Primatology*, *69*(2), 158–172. https://doi.org/10.1002/ajp.20338

Kovács, L., Kézér, F. L., Bakony, M., Jurkovich, V., & Szenci, O. (2018). Lying down frequency as a discomfort index in heat stressed Holstein bull calves. *Scientific Reports*, *8*(1), 15065. https://doi.org/10.1038/s41598-018-33451-6

Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrenschlager, A., & Mason, G. (2016). Stereotypic route tracing in captive Carnivora is predicted by species-typical home range sizes and hunting styles. *Animal Behaviour*, *117*, 197–209. https://doi.org/10.1016/j.anbehav.2016.05.010

Krypotos, A.-M., & Engelhard, I. M. (2018). Testing a novelty-based extinction procedure for the reduction of conditioned avoidance. *Journal of Behavior Therapy and Experimental Psychiatry*, *60*, 22–28. https://doi.org/10.1016/j.jbtep.2018.02.006

Kurtycz, L. M., Wagner, K. E., & Ross, S. R. (2014). The Choice to Access Outdoor Areas Affects the Behavior of Great Apes. *Journal of Applied Animal Welfare Science*, *17*(3), 185–197. https://doi.org/10.1080/10888705.2014.896213

Lagisz, M., Zidar, J., Nakagawa, S., Neville, V., Sorato, E., Paul, E. S., Bateson, M., Mendl, M., & Løvlie, H. (2020). Optimism, pessimism and judgement bias in animals: A systematic review and meta-analysis. *Neuroscience & Biobehavioral Reviews*, *118*, 3–17. https://doi.org/10.1016/j.neubiorev.2020.07.012

Lammey, M. L., Lee, D. R., Ely, J. J., & Sleeper, M. M. (2008). Sudden cardiac death in 13 captive chimpanzees (*Pan troglodytes*). *Journal of Medical Primatology*, *37*, 39–43. https://doi.org/10.1111/j.1600-0684.2007.00260.x

Lamperez, A. J., & Rowell, T. J. (2005). Normal C-reactive protein values for captive chimpanzees (Pan troglodytes). *Contemporary Topics in Laboratory Animal Science*, *44*(5), 25–26.

Laule, G., & Whittaker, M. (2007). Enhancing Nonhuman Primate Care and Welfare Through the Use of Positive Reinforcement Training. *Journal of Applied Animal Welfare Science*, *10*(1), 31–38. https://doi.org/10.1080/10888700701277311

Learmonth, M. J. (2019). Dilemmas for Natural Living Concepts of Zoo Animal Welfare. *Animals*, *9*(6), 318. https://doi.org/10.3390/ani9060318

Lee, P. C., & Strier, K. B. (2015). Complexities of Understanding Female Dispersal in Primates. In T. Furuichi, J. Yamagiwa, & F. Aureli (Eds.), *Dispersing Primate Females* (pp. 215–230). Springer Japan. https://doi.org/10.1007/978-4-431-55480-6_9

Leeds, A., Schook, M. W., Dennis, P. M., Stoinski, T. S., Willis, M. A., & Lukas, K. E. (2023). Urinary oxytocin and cortisol concentrations vary by group type in male western lowland gorillas (Gorilla gorilla gorilla) in North American zoos. *Primates*, *64*(1), 65–77. https://doi.org/10.1007/s10329-022-01037-6

Lewton, K. L. (2017). The effects of captive versus wild rearing environments on long bone articular surfaces in common chimpanzees (*Pan troglodytes*). *PeerJ*, *5*, e3668. https://doi.org/10.7717/peerj.3668

Lutz, C. K., & Baker, K. C. (2023a). Using Behavior to Assess Primate Welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare* (pp. 171–205). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_8

Lutz, C. K., & Baker, K. C. (2023b). Using Behavior to Assess Primate Welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare* (pp. 171–205). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_8

Lyman, R. L. (2008). *Quantitative paleozoology*. Cambridge University Press.

Macdonald, H. M. (2013). Contributions of Sunlight and Diet to Vitamin D Status. *Calcified Tissue International*, *92*(2), 163–176. https://doi.org/10.1007/s00223-012-9634-1

Magden, E. R., Haller, R. L., Thiele, E. J., Buchl, S. J., Lambeth, S. P., & Schapiro, S. J. (2013). Acupuncture as an Adjunct Therapy for Osteoarthritis in Chimpanzees (Pan troglodytes). *Journal of the American Association for Laboratory Animal Science*, *4*, 475–480.

Mallapur, A., Waran, N., & Sinha, A. (2005). Use of Enclosure Space by Captive Lion-Tailed Macaques (Macaca silenus) Housed in Indian Zoos. *Journal of Applied Animal Welfare Science*, *8*(3), 175–186. https://doi.org/10.1207/s15327604jaws0803_2

Masi, S. (2011). Differences in gorilla nettle-feeding between captivity and the wild: Local traditions, species typical behaviors or merely the result of nutritional deficiencies? *Animal Cognition*, *14*(6), 921–925. https://doi.org/10.1007/s10071-011-0457-7

Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, *102*(3–4), 163–188. https://doi.org/10.1016/j.applanim.2006.05.041

Mason, G. J. (1991). Stereotypies: A critical review. *Animal Behaviour*, *41*(6), 1015–1037. https://doi.org/10.1016/S0003-3472(05)80640-2

Mason, G. J. (2010). Species differences in responses to captivity: Stress, welfare and the comparative method. *Trends in Ecology & Evolution*, *25*(12), 713–721. https://doi.org/10.1016/j.tree.2010.08.011

Massen, J. J. M., Antonides, A., Arnold, A.-M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments: Behavioral Measures of Chimp Personality. *American Journal of Primatology*, *75*(9), 947–958. https://doi.org/10.1002/ajp.22159

Maurice, M. E., Gildas, O. A. F., Ekale, B. N., & Fawoh, J. J. (2020). The Activity Budget of Adult Chimpanzees (Pan troglodytes troglodytes) and Environmental Conditions in Mefou Primate Sanctuary, Centre Region, Cameroon. *Asian Journal of Research in Zoology*, 13–25. https://doi.org/10.9734/ajriz/2020/v3i130080

Mayer, F., Scharhag-Rosenberger, F., Carlsohn, A., Cassel, M., Müller, S., & Scharhag, J. (2011). The Intensity and Effects of Strength Training in the Elderly. *Deutsches Ärzteblatt International*. https://doi.org/10.3238/arztebl.2011.0359

Meagher, R. (2019). Is boredom an animal welfare concern? *Animal Welfare*, *28*(1), 21–32. https://doi.org/10.7120/09627286.28.1.021

Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, *102*(3–4), 246–261. https://doi.org/10.1016/j.applanim.2006.05.031

Mellor, D. (2015). Positive animal welfare states and encouraging environment-focused and animal-to-animal interactive behaviours. *New Zealand Veterinary Journal*, *63*(1), 9–16. https://doi.org/10.1080/00480169.2014.926800

Mellor, D. (2016). Moving beyond the “Five Freedoms” by Updating the “Five Provisions” and Introducing Aligned “Animal Welfare Aims.” *Animals*, *6*(10), 59. https://doi.org/10.3390/ani6100059

Meulman, E. J. M., Sanz, C. M., Visalberghi, E., & van Schaik, C. P. (2012). The Role of Terrestriality in Promoting Primate Technology. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(2), 58–68. https://doi.org/10.1002/evan.21304

Miller, L. J., Vicino, G. A., Sheftel, J., & Lauderdale, L. K. (2020). Behavioral Diversity as a Potential Indicator of Positive Animal Welfare. *Animals*, *10*(7), 1211. https://doi.org/10.3390/ani10071211

Mitani, J., & Amsler, S. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884. https://doi.org/10.1163/156853903770238355

Moberg, G. P. (2000). Biological response to stress: Implications for animal welfare. In G. P. Moberg & J. A. Mench (Eds.), *The biology of animal stress: Basic principles and implications for animal welfare.* (1st ed., pp. 1–21). CABI Publishing. https://doi.org/10.1079/9780851993591.0001

Moittié, S., Jarvis, R., Bandelow, S., Byrne, S., Dobbs, P., Grant, M., Reeves, C., White, K., Liptovszky, M., & Baiker, K. (2022). Vitamin D status in chimpanzees in human care: A Europe wide study. *Scientific Reports*, *12*(1), 17625. https://doi.org/10.1038/s41598-022-21211-6

Morimura, N., & Mori, Y. (2010). Effects of early rearing conditions on problem-solving skill in captive male chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, n/a-n/a. https://doi.org/10.1002/ajp.20819

Myatt, J. P., Crompton, R. H., Payne-Davis, R. C., Vereecke, E. E., Isler, K., Savage, R., D'Août, K., Günther, M. M., & Thorpe, S. K. S. (2012). Functional adaptations in the forelimb muscles of non-human great apes: Forelimb muscle architecture in non-human great apes. *Journal of Anatomy*, *220*(1), 13–28. https://doi.org/10.1111/j.1469-7580.2011.01443.x

Myatt, J. P., & Thorpe, S. K. S. (2011). Postural strategies employed by orangutans (Pongo abelii) during feeding in the terminal branch niche. *American Journal of Physical Anthropology*, *146*(1), 73–82. https://doi.org/10.1002/ajpa.21548

Neal Webb, S., Hau, J., & Schapiro, S. (2018). Refinements to captive chimpanzee (Pan troglodytes) care: A selfmedication paradigm. *Animal Welfare*, *27*(4), 327–341. https://doi.org/10.7120/09627286.27.4.327

Neal Webb, S. J., Bridges, J. P., Thiele, E., Lambeth, S. P., & Schapiro, S. J. (2020). The implementation and initial evaluation of a physical therapy program for captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *82*(3). https://doi.org/10.1002/ajp.23109

Neal Webb, S. J., Hau, J., Lambeth, S. P., & Schapiro, S. J. (2019). Differences in Behavior Between Elderly and Nonelderly Captive Chimpanzees and the Effects of the Social Environment. *Journal of the American Association for Laboratory Animal Science*, *58*(6), 783–789. https://doi.org/10.30802/AALAS-JAALAS-19-000019

Neal Webb, S. J., Hau, J., & Schapiro, S. J. (2018). Captive chimpanzee (*Pan troglodytes*) behavior as a function of space per animal and enclosure type. *American Journal of Primatology*, *80*(3), e22749. https://doi.org/10.1002/ajp.22749

Neal Webb, S., & Schapiro, S. (2023). Locomotion as a Measure of Well-Being in Captive Chimpanzees (Pan troglodytes). *Animals*, *13*(5), 803. https://doi.org/10.3390/ani13050803

Neufuss, J., Robbins, M. M., Baeumer, J., Humle, T., & Kivell, T. L. (2017). Comparison of hand use and forelimb posture during vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, *164*(4), 651–664. https://doi.org/10.1002/ajpa.23303

Neufuss, J., Robbins, M. M., Baeumer, J., Humle, T., & Kivell, T. L. (2018). Gait characteristics of vertical climbing in mountain gorillas and chimpanzees. *Journal of Zoology*, *306*(2), 129–138. https://doi.org/10.1111/jzo.12577

Newton-Fisher, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda: Diet of Budongo chimpanzees. *African Journal of Ecology*, *37*(3), 344–354. https://doi.org/10.1046/j.1365-2028.1999.00186.x

Nieuwenhuijsen, K., & de Waal, F. B. M. (1982). Effects of spatial crowding on social behavior in a chimpanzee colony. *Zoo Biology*, *1*(1), 5–28. https://doi.org/10.1002/zoo.1430010103

NIH. (2014). *Notice of Agency Decision: The Density of the Primary Living Space of Captive Chimpanzees Owned or Supported by the NIH or Used in NIH-Supported Research*. https://grants.nih.gov/grants/guide/notice-files/NOT-OD-14-051.html

NIH.gov (2015, November 17). NIH Will No Longer Support Biomedical Research on Chimpanzees. Retrieved from *Https://www.nih.gov/about-nih/who-we-are/nih-director/statements/nih-will-no-longer-support-biomedical-research-chimpanzees*

Novak, M. A., Hamel, A. F., Kelly, B. J., Dettmer, A. M., & Meyer, J. S. (2013). Stress, the HPA axis, and nonhuman primate well-being: A review. *Applied Animal Behaviour Science*, *143*(2–4), 135–149. https://doi.org/10.1016/j.applanim.2012.10.012

Nunamaker, E. A., Lee, D. R., & Lammey, M. L. (2012). Chronic diseases in captive geriatric female Chimpanzees (Pan troglodytes). *Comparative Medicine*, *62*(2), 131–136.

Nybo, L., Rasmussen, P., & Sawka, M. N. (2014). Performance in the Heat—Physiological Factors of Importance for Hyperthermia-Induced Fatigue. In R. Terjung (Ed.), *Comprehensive Physiology* (1st ed., pp. 657–689). Wiley. https://doi.org/10.1002/cphy.c130012

Obanda, V., Omondi, G. P., & Chiyo, P. I. (2014). The Influence of Body Mass Index, Age and Sex on Inflammatory Disease Risk in Semi-Captive Chimpanzees. *PLoS ONE*, *9*(8), e104602. https://doi.org/10.1371/journal.pone.0104602

O'Neill, M. C., Lee, L.-F., Demes, B., Thompson, N. E., Larson, S. G., Stern, J. T., & Umberger, B. R. (2015). Three-dimensional kinematics of the pelvis and hind limbs in chimpanzee (Pan troglodytes) and human bipedal walking. *Journal of Human Evolution*, *86*, 32–42. https://doi.org/10.1016/j.jhevol.2015.05.012

Otovic, P., & Hutchinson, E. (2015). Limits to using HPA axis activity as an indication of animal welfare. *ALTEX*, 41–50. https://doi.org/10.14573/altex.1406161

Palagi, E., & Cordoni, G. (2012). The Right Time to Happen: Play Developmental Divergence in the Two Pan Species. *PLoS ONE*, *7*(12), e52767. https://doi.org/10.1371/journal.pone.0052767

Palme, R. (2019). Non-invasive measurement of glucocorticoids: Advances and problems. *Physiology & Behavior*, *199*, 229–243. https://doi.org/10.1016/j.physbeh.2018.11.021

Palme, R., Rettenbacher, S., Touma, C., El-Bahr, S. M., & Möstl, E. (2005). Stress Hormones in Mammals and Birds: Comparative Aspects Regarding Metabolism, Excretion, and Noninvasive Measurement in Fecal Samples. *Annals of the New York Academy of Sciences*, *1040*(1), 162–171. https://doi.org/10.1196/annals.1327.021

Parr, L. A., & Waller, B. M. (2006). Understanding chimpanzee facial expression: Insights into the evolution of communication. *Social Cognitive and Affective Neuroscience*, *1*(3), 221–228. https://doi.org/10.1093/scan/nsl031

Patel, B. A. (2009). The interplay between speed, kinetics, and hand postures during primate terrestrial locomotion. *American Journal of Physical Anthropology*, NA-NA. https://doi.org/10.1002/ajpa.21138

Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (Pan troglodytes) personality predicts behavior. *Journal of Research in Personality*, *39*(5), 534–549. https://doi.org/10.1016/j.jrp.2004.07.002

Pizzutto, C. S., Sgai, M. G. F. G., Lopes, D. A., Pessutti, C., Nunes, A., Furtado, P. V., Oliveira, C. A. de, & Guimarães, M. A. B. V. (2015). Relation between the level of self-mutilation and theconcentration of fecal metabolites of glucocorticoids incaptive chimpanzees (Pan troglodytes). *Pesquisa Veterinária Brasileira*, *35*(1), 62–66. https://doi.org/10.1590/S0100-736X2015000100013

Pomerantz, O., Terkel, J., Suomi, S. J., & Paukner, A. (2012). Stereotypic head twirls, but not pacing, are related to a ‘pessimistic’-like judgment bias among captive tufted capuchins (Cebus apella). *Animal Cognition*, *15*(4), 689–698. https://doi.org/10.1007/s10071-012-0497-7

Pontzer, H., & Wrangham, R. W. (2004). Climbing and the daily energy cost of locomotion in wild chimpanzees: Implications for hominoid locomotor evolution. *Journal of Human Evolution*, *46*(3), 315–333. https://doi.org/10.1016/j.jhevol.2003.12.006

Potts, R. (2004). Paleoenvironmental basis of cognitive evolution in great apes. *American Journal of Primatology*, *62*(3), 209–228. https://doi.org/10.1002/ajp.20016

Pressman, S. D., & Cohen, S. (2005). Does positive affect influence health? *Psychological Bulletin*, *131*(6), 925–971. https://doi.org/10.1037/0033-2909.131.6.925

Preuschoft, H. (2002). What does “arboreal locomotion” mean exactly and what are the relationships between “climbing”, environment and morphology? *Zeitschrift Fur Morphologie Und Anthropologie*, *83*(2–3), 171–188.

Proudfit, G. H., Bress, J. N., Foti, D., Kujawa, A., & Klein, D. N. (2015). Depression and event-related potentials: Emotional disengagement and reward insensitivity. *Current Opinion in Psychology*, *4*, 110–113. https://doi.org/10.1016/j.copsyc.2014.12.018

Pruetz, J. D. (2018). Nocturnal behavior by a diurnal ape, the West African chimpanzee (*Pan troglodytes verus*), in a savanna environment at Fongoli, Senegal. *American Journal of Physical Anthropology*, *166*(3), 541–548. https://doi.org/10.1002/ajpa.23434

Pruetz, J. D., Fulton, S. J., Marchant, L. F., McGrew, W. C., Schiel, M., & Waller, M. (2008). Arboreal nesting as anti-predator adaptation by savanna chimpanzees (Pan troglodytes verus) in southeastern Senegal. *American Journal of Primatology*, *70*(4), 393–401. https://doi.org/10.1002/ajp.20508

Ramos-Fernandez, G., King, A. J., Beehner, J. C., Bergman, T. J., Crofoot, M. C., Di Fiore, A., Lehmann, J., Schaffner, C. M., Snyder-Mackler, N., Zuberbühler, K., Aureli, F., & Boyer, D. (2018). Quantifying uncertainty due to fission–fusion dynamics as a component of social complexity. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1879), 20180532. https://doi.org/10.1098/rspb.2018.0532

Reamer, L. A., Neal Webb, S. J., Jones, R., Thiele, E., Haller, R. L., Schapiro, S. J., Lambeth, S. P., & Hanley, P. W. (2020). Validation and utility of a body condition scoring system for chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *82*(10). https://doi.org/10.1002/ajp.23188

Reamer, L., Tooze, Z., Coulson, C., & Semple, S. (2010). Correlates of self-directed and stereotypic behaviours in captive red-capped mangabeys (Cercocebus torquatus torquatus). *Applied Animal Behaviour Science*, *124*(1–2), 68–74. https://doi.org/10.1016/j.applanim.2010.01.012

Reardon, S. (2015). NIH to retire all research chimpanzees. *Nature*, nature.2015.18817. https://doi.org/10.1038/nature.2015.18817

Robinson, L. M., Waran, N. K., Leach, M. C., Morton, F. B., Paukner, A., Lonsdorf, E., Handel, I., Wilson, V. A. D., Brosnan, S. F., & Weiss, A. (2016). Happiness is positive welfare in brown capuchins (Sapajus apella). *Applied Animal Behaviour Science*, *181*, 145–151. https://doi.org/10.1016/j.applanim.2016.05.029

Robinson, L. M., & Weiss, A. (2023). Primate Personality and Welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare* (pp. 395–411). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_17

Romero, L. M. (2004). Physiological stress in ecology: Lessons from biomedical research. *Trends in Ecology & Evolution*, *19*(5), 249–255. https://doi.org/10.1016/j.tree.2004.03.008

Ross, S. R., Bloomsmith, M. A., Bettinger, T. L., & Wagner, K. E. (2009). The influence of captive adolescent male chimpanzees on wounding: Management and welfare implications. *Zoo Biology*, n/a-n/a. https://doi.org/10.1002/zoo.20243

Ross, S. R., Calcutt, S., Schapiro, S. J., & Hau, J. (2011). Space use selectivity by chimpanzees and gorillas in an indoor-outdoor enclosure. *American Journal of Primatology*, *73*(2), 197–208. https://doi.org/10.1002/ajp.20891

Ross, S. R., Lake, B. R., Fultz, A., & Hopper, L. M. (2021). An evaluation of thermal imaging as a welfare monitoring tool for captive chimpanzees. *Primates*, *62*(6), 919–927. https://doi.org/10.1007/s10329-021-00943-5

Ross, S. R., & Lukas, K. E. (2006). Use of space in a non-naturalistic environment by chimpanzees (Pan troglodytes) and lowland gorillas (Gorilla gorilla gorilla). *Applied Animal Behaviour Science*, *96*(1–2), 143–152. https://doi.org/10.1016/j.applanim.2005.06.005

Ross, S. R., Schapiro, S. J., Hau, J., & Lukas, K. E. (2009). Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. *Applied Animal Behaviour Science*, *121*(1), 42–50. https://doi.org/10.1016/j.applanim.2009.08.007

Ross, S. R., & Shender, M. A. (2016). Daily travel distances of zoo-housed chimpanzees and gorillas: Implications for welfare assessments and space requirements. *Primates*, *57*(3), 395–401. https://doi.org/10.1007/s10329-016-0530-6

Ross, S. R., Wagner, K. E., Schapiro, S. J., & Hau, J. (2010). Ape behavior in two alternating environments: Comparing exhibit and short-term holding areas. *American Journal of Primatology*, *72*(11), 951–959. https://doi.org/10.1002/ajp.20857

Samuel, D. S., Nauwelaerts, S., Stevens, J. M. G., & Kivell, T. L. (2018). Hand pressures during arboreal locomotion in captive bonobos (*Pan paniscus*). *Journal of Experimental Biology*, jeb.170910. https://doi.org/10.1242/jeb.170910

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888), 20181643. https://doi.org/10.1098/rspb.2018.1643

Sarringhaus, L. A. (2013). *Positional and Morphological Development of Wild Chimpanzees*. The University of Michigan.

Sarringhaus, L. A., MacLatchy, L. M., & Mitani, J. C. (2014). Locomotor and postural development of wild chimpanzees. *Journal of Human Evolution*, *66*, 29–38. https://doi.org/10.1016/j.jhevol.2013.09.006

Satariano, W. A., Guralnik, J. M., Jackson, R. J., Marottoli, R. A., Phelan, E. A., & Prohaska, T. R. (2012). Mobility and aging: New directions for public health action. *American Journal of Public Health*, *102*(8), 1508–1515. https://doi.org/10.2105/AJPH.2011.300631

Saunders, E. L. R., Roberts, A. M., & Thorpe, S. K. S. (2017). Positional Behavior. In M. Bezanson, K. C. MacKinnon, E. Riley, C. J. Campbell, K. A. I. A. Nekaris, A. Estrada, A. F. Di Fiore, S. Ross, L. E. Jones-Engel, B. Thierry, R. W. Sussman, C. Sanz, J. Loudon, S. Elton, & A. Fuentes (Eds.), *The International Encyclopedia of Primatology* (pp. 1–14). John Wiley & Sons, Inc. https://doi.org/10.1002/9781119179313.wbprim0074

Schapiro, S. J., & Lambeth, S. P. (2007). Control, Choice, and Assessments of the Value of Behavioral Management to Nonhuman Primates in Captivity. *Journal of Applied Animal Welfare Science*, *10*(1), 39–47. https://doi.org/10.1080/10888700701277345

Scheveneels, S., Boddez, Y., Vervliet, B., & Hermans, D. (2016). The validity of laboratory-based treatment research: Bridging the gap between fear extinction and exposure treatment. *Behaviour Research and Therapy*, *86*, 87–94. https://doi.org/10.1016/j.brat.2016.08.015

Schmidt, A. T. (2015). Warum Tiere ein Interesse an Freiheit habenWhy Animals have an Interest in Freedom. *Historical Social Research / Historische Sozialforschung Vol. 40*, *No. 4* https://doi.org/10.12759/HSR.40.2015.4.92-109

Schmidt, M. (2011). Locomotion and postural behaviour. *Advances in Science and Research*, *5*(1), 23–39. https://doi.org/10.5194/asr-5-23-2010

Schoonaert, K., D’Août, K., Samuel, D., Talloen, W., Nauwelaerts, S., Kivell, T. L., & Aerts, P. (2016). Gait characteristics and spatio-temporal variables of climbing in bonobos (*Pan paniscus*): Gait Aspects of Climbing in Bonobos. *American Journal of Primatology*, *78*(11), 1165–1177. https://doi.org/10.1002/ajp.22571

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour*, *103*, 191–202. https://doi.org/10.1016/j.anbehav.2015.01.030

Sha, J. C. M., Ismail, R., Marlena, D., & Lee, J. L. (2016). Environmental complexity and feeding enrichment can mitigate effects of space constraints in captive callitrichids. *Laboratory Animals*, *50*(2), 137–144. https://doi.org/10.1177/0023677215589258

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Shutt, K., MacLarnon, A., Heistermann, M., & Semple, S. (2007). Grooming in Barbary macaques: Better to give than to receive? *Biology Letters*, *3*(3), 231–233. https://doi.org/10.1098/rsbl.2007.0052

Sidlauskiene, A., Strukcinskiene, B., Raistenskis, J., Stukas, R., Strukcinskaite, V., & Buckus, R. (2019). The association between the level of physical activity with spinal posture and physical fitness parameters in early adolescence. *Vojnosanitetski Pregled*, *76*(12), 1209–1216. https://doi.org/10.2298/VSP170517098S

Skyner, L. J., Amory, J. R., & Hosey, G. (2004). *The Effect of Visitors on Self-Injurious Behaviour of a Male Pileated Gibbon (Hylobates pileatus)*.

Smith, A. L., Benazzi, S., Ledogar, J. A., Tamvada, K., Pryor Smith, L. C., Weber, G. W., Spencer, M. A., Dechow, P. C., Grosse, I. R., Ross, C. F., Richmond, B. G., Wright, B. W., Wang, Q., Byron, C., Slice, D. E., & Strait, D. S. (2015). Biomechanical Implications of Intraspecific Shape Variation in Chimpanzee Crania: Moving Toward an Integration of Geometric Morphometrics and Finite Element Analysis: INTRASPECIFIC SHAPE VARIATION IN CHIMPANZEE CRANIA. *The Anatomical Record*, *298*(1), 122–144. https://doi.org/10.1002/ar.23074

Sockol, M. D., Raichlen, D. A., & Pontzer, H. (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *Proceedings of the National Academy of Sciences*, *104*(30), 12265–12269. https://doi.org/10.1073/pnas.0703267104

Song, J., Wu, Z., Wang, J., Zhang, K., Wang, K., Liu, K., Duan, L., & Hou, H. (2021). Application of highly concentrated sunlight transmission and daylighting indoor via plastic optical fibers with comprehensive cooling approaches. *Renewable Energy*, *180*, 1391–1404. https://doi.org/10.1016/j.renene.2021.08.112

Soubiea, H. A. (2017). C*himpanzee (Pan troglodytes) space use in a sanctuary setting. Central Washington University.*

Soylu, G., Çakmak, G., Yalvaç, Y., Yakaryılmaz, F. D., & Öztürk, Z. A. (2021). Relationship Between Age-Related Postural Hyperkyphosis and Sarcopenia. *Current Aging Science*, *14*(2), 133–138. https://doi.org/10.2174/1874609814666210322114500

Spiezio, C., Vaglio, S., Vandelle, C., Sandri, C., & Regaiolli, B. (2021). Effects of Rearing on the Behaviour of Zoo-Housed Chimpanzees (Pan troglodytes). *Folia Primatologica*, *92*(2), 91–102. https://doi.org/10.1159/000515127

Spijkerman, R. P., Dienske, H., van Hooff, J. A. R. A. M., & Jens, W. (1994). Causes of Body Rocking in Chimpanzees (*Pan Troglodytes*). *Animal Welfare*, *3*(3), 193–211. https://doi.org/10.1017/S0962728600016845

Špinka, M. (2019). Animal agency, animal awareness and animal welfare. *Animal Welfare*, *28*(1), 11–20. https://doi.org/10.7120/09627286.28.1.011

Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian Play: Training for the Unexpected. *The Quarterly Review of Biology*, *76*(2), 141–168. https://doi.org/10.1086/393866

Staley, M., Conners, M. G., Hall, K., & Miller, L. J. (2018). Linking stress and immunity: Immunoglobulin A as a non-invasive physiological biomarker in animal welfare studies. *Hormones and Behavior*, *102*, 55–68. https://doi.org/10.1016/j.yhbeh.2018.04.011

Stewart, F. A., & Pruetz, J. D. (2013). Do Chimpanzee Nests Serve an Anti-Predatory Function?: Anti-Predatory Nest Function. *American Journal of Primatology*, *75*(6), 593–604. https://doi.org/10.1002/ajp.22138

Stewart, F. A., Pruetz, J. D., & Hansell, M. H. (2007). Do chimpanzees build comfortable nests? *American Journal of Primatology*, *69*(8), 930–939. https://doi.org/10.1002/ajp.20432

Stoinski, T. S., Hoff, M. P., & Maple, T. L. (2001). Habitat Use and Structural Preferences of Captive Western Lowland Gorillas (Gorilla gorilla gorilla(: Effects of Environmental and Social Variables. *International Journal of Primatology*, *22*(3), 431–447. https://doi.org/10.1023/A:1010707712728

Street, S. E., Navarrete, A. F., Reader, S. M., & Laland, K. N. (2017). Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of the National Academy of Sciences*, *114*(30), 7908–7914. https://doi.org/10.1073/pnas.1620734114

Strier, K. B. (2017). *Primate behavioral ecology* (Fifth edition). Routledge, Taylor & Francis Group.

Strong, V., Moittié, S., Sheppard, M. N., Liptovszky, M., White, K., Redrobe, S., Cobb, M., & Baiker, K. (2020). Idiopathic Myocardial Fibrosis in Captive Chimpanzees (*Pan troglodytes*). *Veterinary Pathology*, *57*(1), 183–191. https://doi.org/10.1177/0300985819879442

Sussman, R. W., Tab Rasmussen, D., & Raven, P. H. (2013). Rethinking Primate Origins Again: Primate Origins Again. *American Journal of Primatology*, *75*(2), 95–106. https://doi.org/10.1002/ajp.22096

Tacconi, G., & Palagi, E. (2009). Play behavioural tactics under space reduction: Social challenges in bonobos, Pan paniscus. *Animal Behaviour*, *78*(2), 469–476. https://doi.org/10.1016/j.anbehav.2009.06.004

Thorpe, S. K. S., & Crompton, R. H. (2006). Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. *American Journal of Physical Anthropology*, *131*(3), 384–401. https://doi.org/10.1002/ajpa.20422

Touma, C., & Palme, R. (2005). Measuring Fecal Glucocorticoid Metabolites in Mammals and Birds: The Importance of Validation. *Annals of the New York Academy of Sciences*, *1046*(1), 54–74. https://doi.org/10.1196/annals.1343.006

Trapanese, C., Meunier, H., & Masi, S. (2019). What, where and when: Spatial foraging decisions in primates: Spatial foraging decisions in primates. *Biological Reviews*, *94*(2), 483–502. https://doi.org/10.1111/brv.12462

Traylor-Holzer, K., & Fritz, P. (1985). Utilization of space by adult and juvenile groups of captive chimpanzees (Pan troglodytes). *Zoo Biology*, *4*(2), 115–127. https://doi.org/10.1002/zoo.1430040205

Turner, P. V. (2023). The History of Chimpanzees in Biomedical Research. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare* (pp. 31–55). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_2

Varki, N., Anderson, D., Herndon, J. G., Pham, T., Gregg, C. J., Cheriyan, M., Murphy, J., Strobert, E., Fritz, J., Else, J. G., & Varki, A. (2009). ORIGINAL ARTICLE: Heart disease is common in humans and chimpanzees, but is caused by different pathological processes: Heart disease in hominids. *Evolutionary Applications*, *2*(1), 101–112. https://doi.org/10.1111/j.1752-4571.2008.00064.x

Veasey, J. S. (2017). In pursuit of peak animal welfare; the need to prioritize the meaningful over the measurable. *Zoo Biology*, *36*(6), 413–425. https://doi.org/10.1002/zoo.21390

Vick, S.-J., & Paukner, A. (2010). Variation and context of yawns in captive chimpanzees (Pan troglodytes). *American Journal of Primatology*, *72*(3), 262–269. https://doi.org/10.1002/ajp.20781

Videan, E. N., & Fritz, J. (2007). Effects of short- and long-term changes in spatial density on the social behavior of captive chimpanzees (Pan troglodytes). *Applied Animal Behaviour Science*, *102*(1–2), 95–105. https://doi.org/10.1016/j.applanim.2006.03.011

Vieira, W. F., Kerry, C., & Hockings, K. J. (2019). A comparison of methods to determine chimpanzee home-range size in a forest–farm mosaic at Madina in Cantanhez National Park, Guinea-Bissau. *Primates*, *60*(4), 355–365. https://doi.org/10.1007/s10329-019-00724-1

Vogel, T., Brechat, P.-H., Leprêtre, P.-M., Kaltenbach, G., Berthel, M., & Lonsdorfer, J. (2009). Health benefits of physical activity in older patients: A review. *International Journal of Clinical Practice*, *63*(2), 303–320. https://doi.org/10.1111/j.1742-1241.2008.01957.x

Waal, F. B. M. de. (2020). *Mama's last hug: Animal emotions and what they tell us about ourselves*. W.W. Norton & Company.

Walker, M., Duggan, G., Roulston, N., Van Slack, A., & Mason, G. (2012). Negative affective states and their effects on morbidity, mortality and longevity. *Animal Welfare*, *21*(4), 497–509. https://doi.org/10.7120/09627286.21.4.497

Watts, D. P. (2006). Conflict Resolution in Chimpanzees and the Valuable-relationships Hypothesis. *International Journal of Primatology*, *27*(5), 1337–1364. https://doi.org/10.1007/s10764-006-9081-9

Watts, D. P. (2022). Male chimpanzee sexual coercion and mating success at Ngogo. *American Journal of Primatology*, *84*(2). https://doi.org/10.1002/ajp.23361

Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, *68*(2), 161–180. https://doi.org/10.1002/ajp.20214

Webster, J. I., Tonelli, L., & Sternberg, E. M. (2002). Neuroendocrine Regulation of Immunity. *Annual Review of Immunology*, *20*(1), 125–163. https://doi.org/10.1146/annurev.immunol.20.082401.104914

Weiss, A., Adams, M. J., & King, J. E. (2011). Happy orang-utans live longer lives. *Biology Letters*, *7*(6), 872–874. https://doi.org/10.1098/rsbl.2011.0543

Whitehouse, J., Micheletta, J., Powell, L. E., Bordier, C., & Waller, B. M. (2013). The Impact of Cognitive Testing on the Welfare of Group Housed Primates. *PLoS ONE*, *8*(11), e78308. https://doi.org/10.1371/journal.pone.0078308

Whitham, J. C., Bryant, J. L., & Miller, L. J. (2020). Beyond Glucocorticoids: Integrating Dehydroepiandrosterone (DHEA) into Animal Welfare Research. *Animals*, *10*(8), 1381. https://doi.org/10.3390/ani10081381

Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., & Justice, W. (2018). Assessment of Welfare in Zoo Animals: Towards Optimum Quality of Life. *Animals*, *8*(7), 110. https://doi.org/10.3390/ani8070110

Wormald, D., Lawrence, A. J., Carter, G., & Fisher, A. D. (2016). Validation of modified open field behaviour as a measure of trait anxiety in the dog. *Applied Animal Behaviour Science*, *179*, 95–102. https://doi.org/10.1016/j.applanim.2016.03.004

Wunderground.com. (n.d.). Shreveport, LA Weather History. Retrieved from *https://www.wunderground.com/history/daily/us/la/shreveport/KSHV/*

Yamanashi, Y. (2018). Is Hair Cortisol Useful for Animal Welfare Assessment? Review of Studies in Captive Chimpanzees. *Aquatic Mammals*, *44*(2), 201–210. https://doi.org/10.1578/AM.44.2.2018.201

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*(12), 1231–1238. https://doi.org/10.1002/ajp.20995

Yamanashi, Y., Morimura, N., Mori, Y., Hayashi, M., & Suzuki, J. (2013). Cortisol analysis of hair of captive chimpanzees (Pan troglodytes). *General and Comparative Endocrinology*, *194*, 55–63. https://doi.org/10.1016/j.ygcen.2013.08.013

Yamanashi, Y., Nogami, E., Teramoto, M., Morimura, N., & Hirata, S. (2018). Adult-adult social play in captive chimpanzees: Is it indicative of positive animal welfare? *Applied Animal Behaviour Science*, *199*, 75–83. https://doi.org/10.1016/j.applanim.2017.10.006

Yamanashi, Y., Teramoto, M., Morimura, N., Hirata, S., Inoue-Murayama, M., & Idani, G. (2016). Effects of Relocation and Individual and Environmental Factors on the Long-Term Stress Levels in Captive Chimpanzees (Pan troglodytes): Monitoring Hair Cortisol and Behaviors. *PLOS ONE*, *11*(7), e0160029. https://doi.org/10.1371/journal.pone.0160029

Yamanashi, Y., Teramoto, M., Morimura, N., Nogami, E., & Hirata, S. (2018). Social relationship and hair cortisol level in captive male chimpanzees (Pan troglodytes). *Primates*, *59*(2), 145–152. https://doi.org/10.1007/s10329-017-0641-8

Yang, C.-J., Liu, D., Xu, Z.-S., Shi, S.-X., & Du, Y.-J. (2017). The pro-inflammatory cytokines, salivary cortisol and alpha-amylase are associated with generalized anxiety disorder (GAD) in patients with asthma. *Neuroscience Letters*, *656*, 15–21. https://doi.org/10.1016/j.neulet.2017.07.021

Yeager, C. P. (1991). Possible antipredator behavior associated with river crossings by proboscis monkeys (Nasalis larvatus). *American Journal of Primatology*, *24*(1), 61–66. https://doi.org/10.1002/ajp.1350240107

Yeates, J. (2018). Naturalness and Animal Welfare. *Animals*, *8*(4), 53. https://doi.org/10.3390/ani8040053

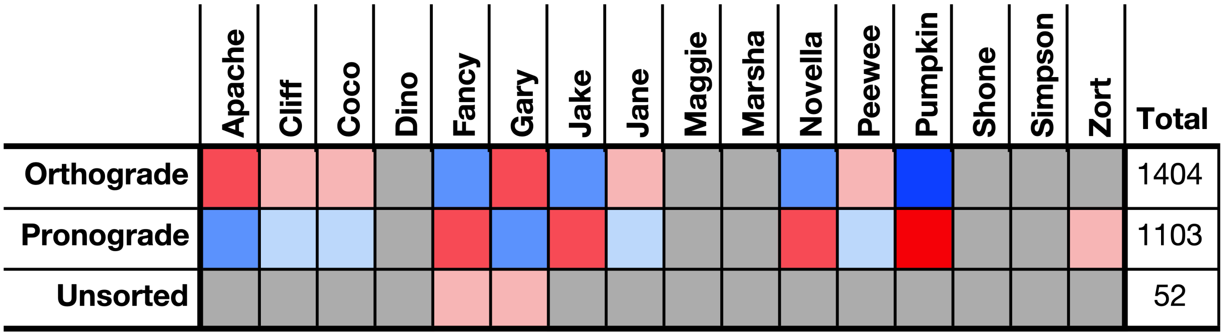
Zihlman, A. L., Stahl, D., & Boesch, C. (2008). Morphological variation in adult chimpanzees (Pan troglodytes verus) of the Taï National Park, Côte d'Ivoire. *American Journal of Physical Anthropology*, *135*(1), 34–41. https://doi.org/10.1002/ajpa.20702

Zizzo, J. (2021). Muscle Atrophy Classification: The Need for a Pathway-Driven Approach. *Current Pharmaceutical Design*, *27*(27), 3012–3019. https://doi.org/10.2174/1381612824666210316102413

Appendices

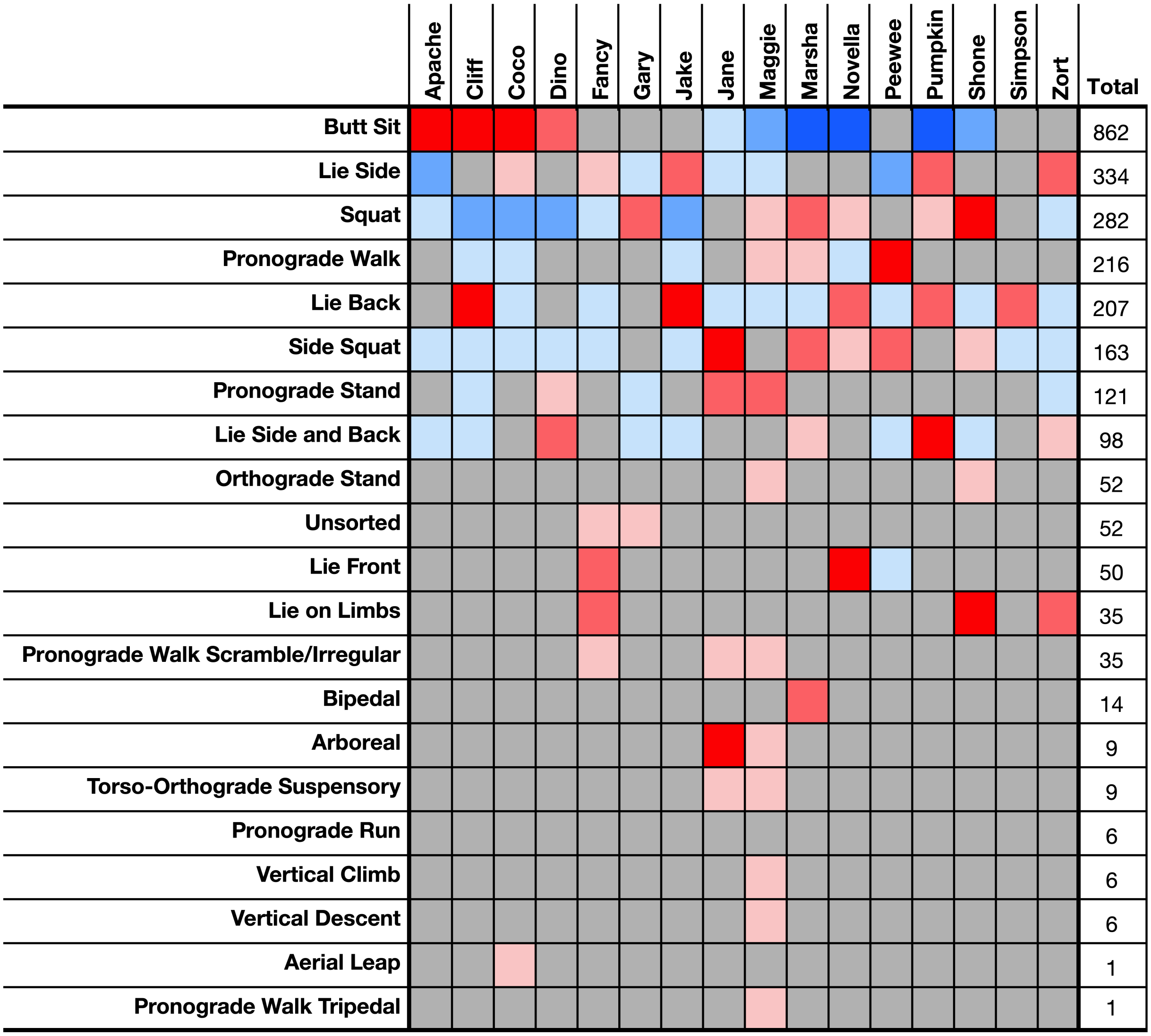
Appendix A: Supplemental Figures

Supplemental Figures S4.2.1



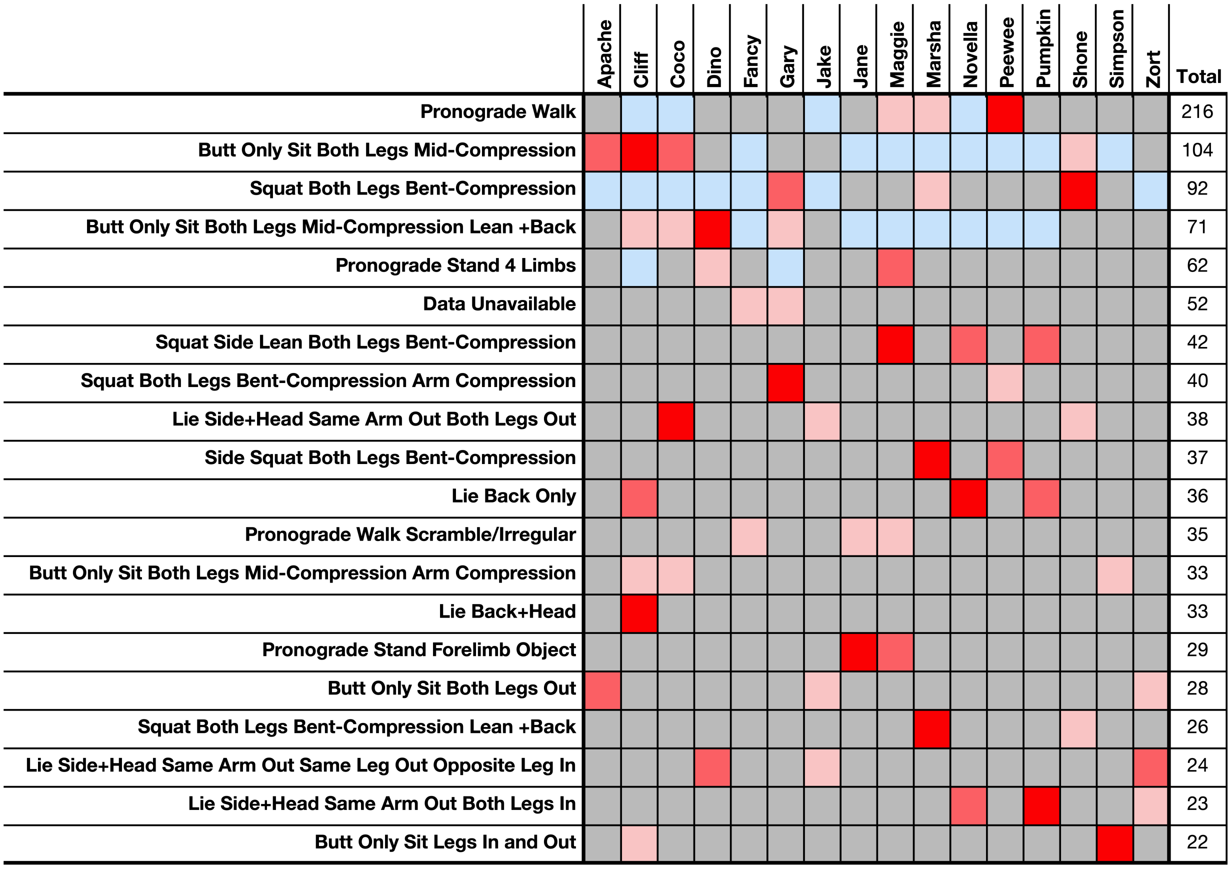
	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort	Total
Orthograde	🟥	🟥	🟥	▨	🟦	🟥	🟦	🟥	▨	▨	🟦	🟥	🟦	▨	▨	▨	1404
Pronograde	🟦	🟦	🟦	▨	🟥	🟦	🟥	🟦	▨	▨	🟥	🟦	🟥	▨	▨	🟥	1103
Unsorted	▨	▨	▨	▨	🟥	🟥	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	52

Figure S4.2.1.1 Subjects displayed different rates of engaging their bodies in orthograde versus pronograde orientations (Chi-square = 230.22, df = 30, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.



	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort	Total
Butt Sit																	862
Lie Side																	334
Squat																	282
Pronograde Walk																	216
Lie Back																	207
Side Squat																	163
Pronograde Stand																	121
Lie Side and Back																	98
Orthograde Stand																	52
Unsorted																	52
Lie Front																	50
Lie on Limbs																	35
Pronograde Walk Scramble/Irregular																	35
Bipedal																	14
Arboreal																	9
Torso-Orthograde Suspensory																	9
Pronograde Run																	6
Vertical Climb																	6
Vertical Descent																	6
Aerial Leap																	1
Pronograde Walk Tripedal																	1

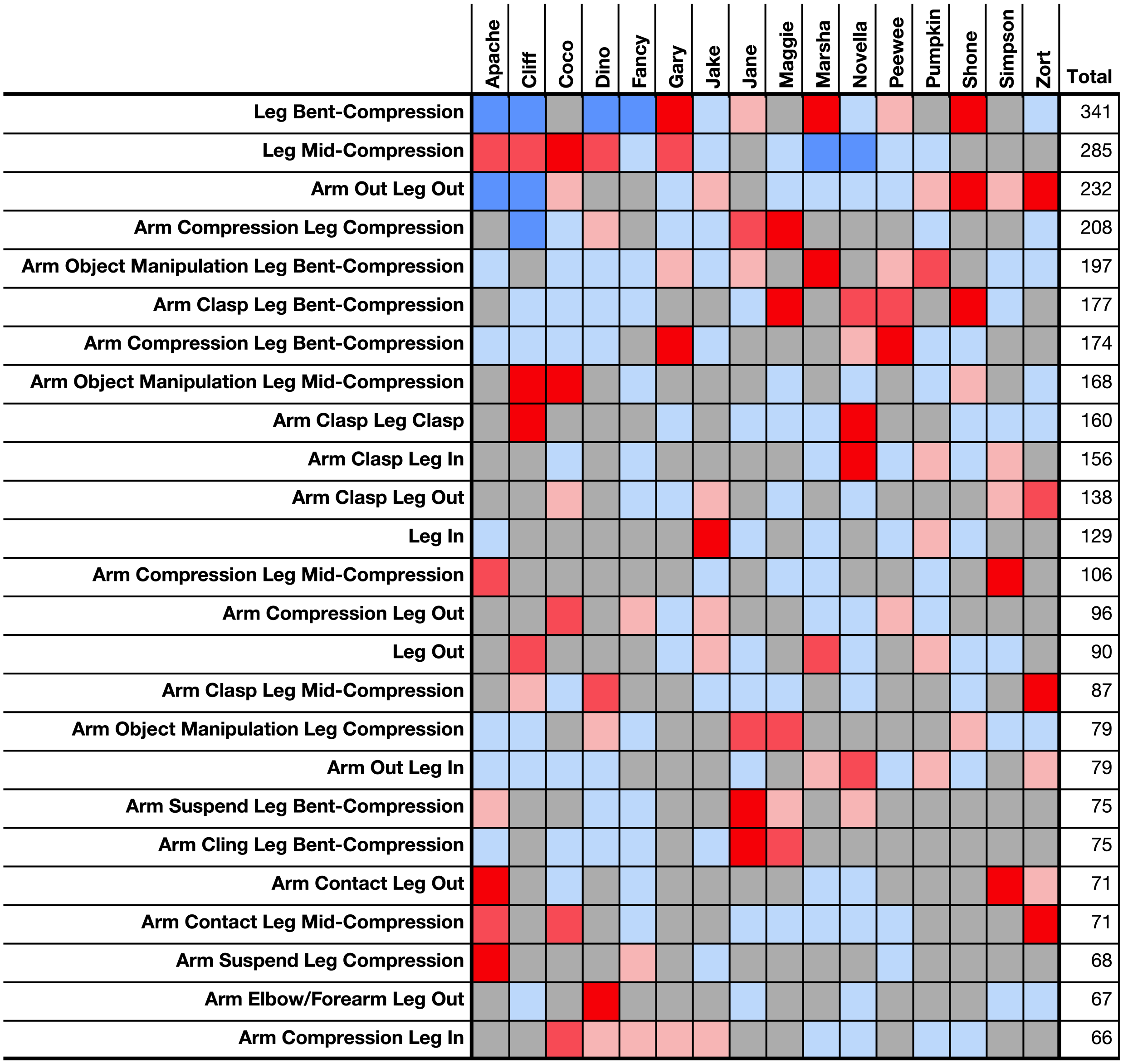
Figure S4.2.1.2 Subjects' profiles of positional behaviors under the Pos7 classification schema. Positional behavior profiles were significantly different between subjects (Chi-square = 1931.3, df = 300, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.
Only the first 20 rows are displayed.



	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort	Total
Pronograde Walk		🟦	🟦				🟦		░	░	🟦	🟥					216
Butt Only Sit Both Legs Mid-Compression	▦	🟥	▦		🟦			🟦	🟦	🟦	🟦	🟦	🟦	░	🟦		104
Squat Both Legs Bent-Compression	🟦	🟦	🟦	🟦	🟦	▦	🟦			░				🟥		🟦	92
Butt Only Sit Both Legs Mid-Compression Lean +Back		░	░	🟥	🟦	░		🟦	🟦	🟦	🟦	🟦	🟦				71
Pronograde Stand 4 Limbs		🟦		░		🟦			▦								62
Data Unavailable					░	░											52
Squat Side Lean Both Legs Bent-Compression									🟥		▦		▦				42
Squat Both Legs Bent-Compression Arm Compression						🟥						░					40
Lie Side+Head Same Arm Out Both Legs Out			🟥				░							░			38
Side Squat Both Legs Bent-Compression										🟥		▦					37
Lie Back Only		▦									🟥		▦				36
Pronograde Walk Scramble/Irregular					░			░	░								35
Butt Only Sit Both Legs Mid-Compression Arm Compression		░	░												░		33
Lie Back+Head		🟥															33
Pronograde Stand Forelimb Object								🟥	▦								29
Butt Only Sit Both Legs Out	▦						░									░	28
Squat Both Legs Bent-Compression Lean +Back										🟥				░			26
Lie Side+Head Same Arm Out Same Leg Out Opposite Leg In				▦			░									▦	24
Lie Side+Head Same Arm Out Both Legs In											▦		🟥			░	23
Butt Only Sit Legs In and Out		░													🟥		22

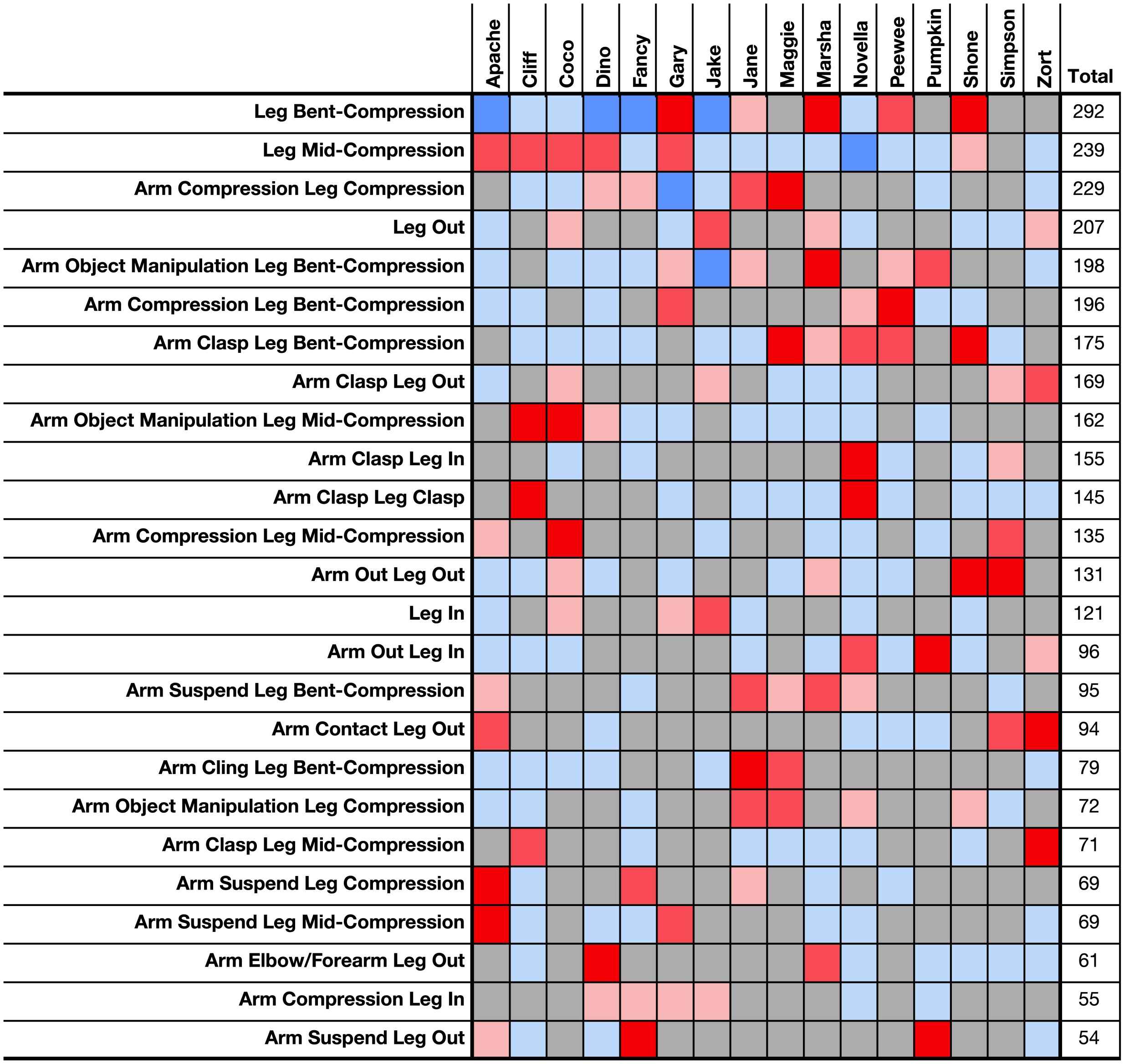
Figure S4.2.1.3 Subjects' profiles of positional behaviors under the Pos1 classification schema. Positional behavior profiles were significantly different between subjects (Chi-square = 16950, df = 7830, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

Supplemental Figures S4.2.2



	Total
Leg Bent-Compression	341
Leg Mid-Compression	285
Arm Out Leg Out	232
Arm Compression Leg Compression	208
Arm Object Manipulation Leg Bent-Compression	197
Arm Clasp Leg Bent-Compression	177
Arm Compression Leg Bent-Compression	174
Arm Object Manipulation Leg Mid-Compression	168
Arm Clasp Leg Clasp	160
Arm Clasp Leg In	156
Arm Clasp Leg Out	138
Leg In	129
Arm Compression Leg Mid-Compression	106
Arm Compression Leg Out	96
Leg Out	90
Arm Clasp Leg Mid-Compression	87
Arm Object Manipulation Leg Compression	79
Arm Out Leg In	79
Arm Suspend Leg Bent-Compression	75
Arm Cling Leg Bent-Compression	75
Arm Contact Leg Out	71
Arm Contact Leg Mid-Compression	71
Arm Suspend Leg Compression	68
Arm Elbow/Forearm Leg Out	67
Arm Compression Leg In	66

Figure S4.2.2.1 The tendencies for simultaneous engagements of ipsilateral limbs were significantly different between subjects (Chi-square = 7625.6, df = 1380, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.



	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort	Total
Leg Bent-Compression																	292
Leg Mid-Compression																	239
Arm Compression Leg Compression																	229
Leg Out																	207
Arm Object Manipulation Leg Bent-Compression																	198
Arm Compression Leg Bent-Compression																	196
Arm Clasp Leg Bent-Compression																	175
Arm Clasp Leg Out																	169
Arm Object Manipulation Leg Mid-Compression																	162
Arm Clasp Leg In																	155
Arm Clasp Leg Clasp																	145
Arm Compression Leg Mid-Compression																	135
Arm Out Leg Out																	131
Leg In																	121
Arm Out Leg In																	96
Arm Suspend Leg Bent-Compression																	95
Arm Contact Leg Out																	94
Arm Cling Leg Bent-Compression																	79
Arm Object Manipulation Leg Compression																	72
Arm Clasp Leg Mid-Compression																	71
Arm Suspend Leg Compression																	69
Arm Suspend Leg Mid-Compression																	69
Arm Elbow/Forearm Leg Out																	61
Arm Compression Leg In																	55
Arm Suspend Leg Out																	54

Figure S4.2.2.2 The tendencies for simultaneous engagements of contralateral limbs were significantly different between subjects (Chi-square = 7915.8, df = 1455, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

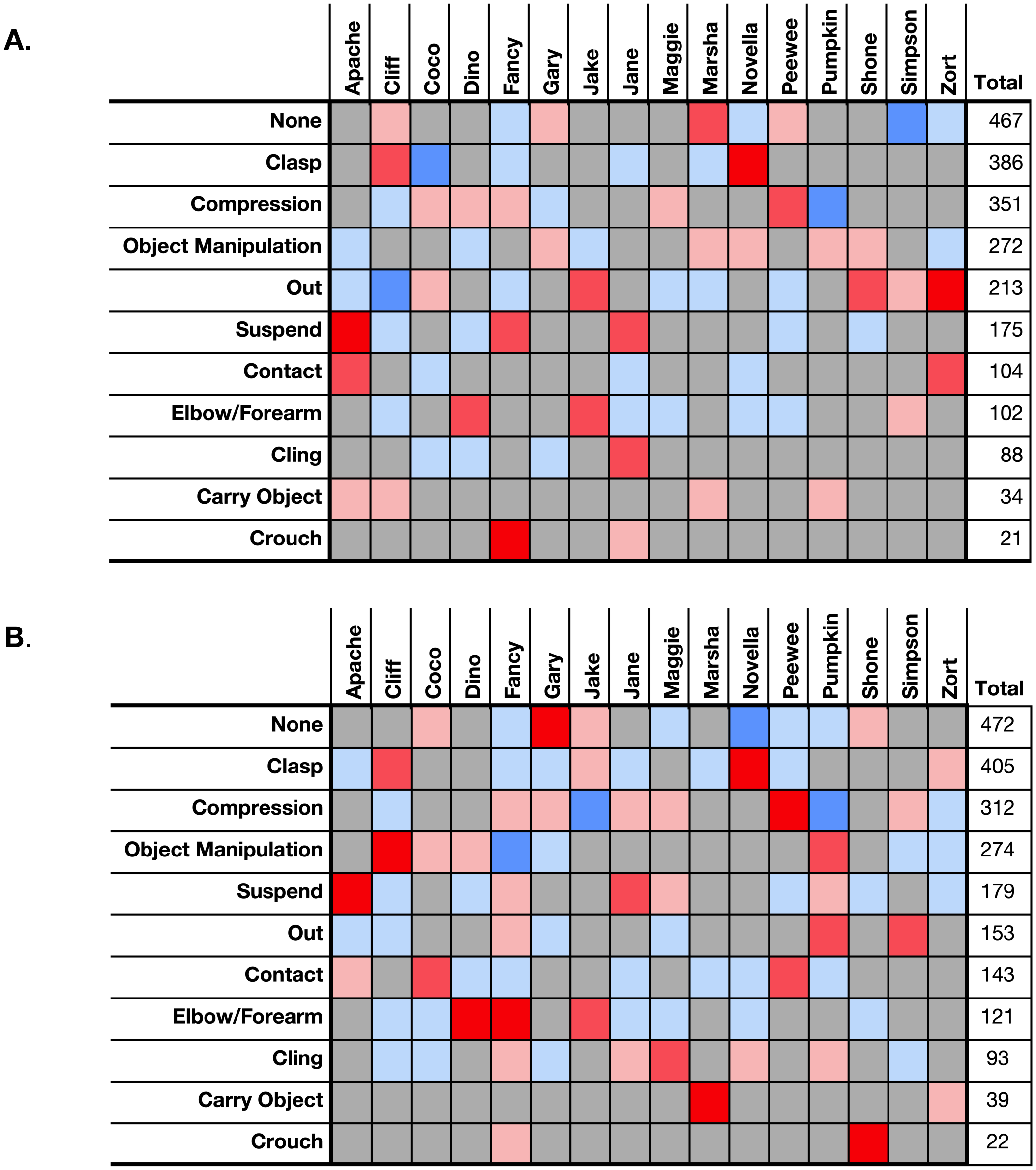


Figure S4.2.2.3 **A**. The differing tendencies for subjects to engage their left arm (Chi-square = 988.66, df = 150, $p < 2.2 \times 10^{-16}$). **B**. The differing tendencies for subjects to engage their right arm (Chi-square = 1199.4, df = 150, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.

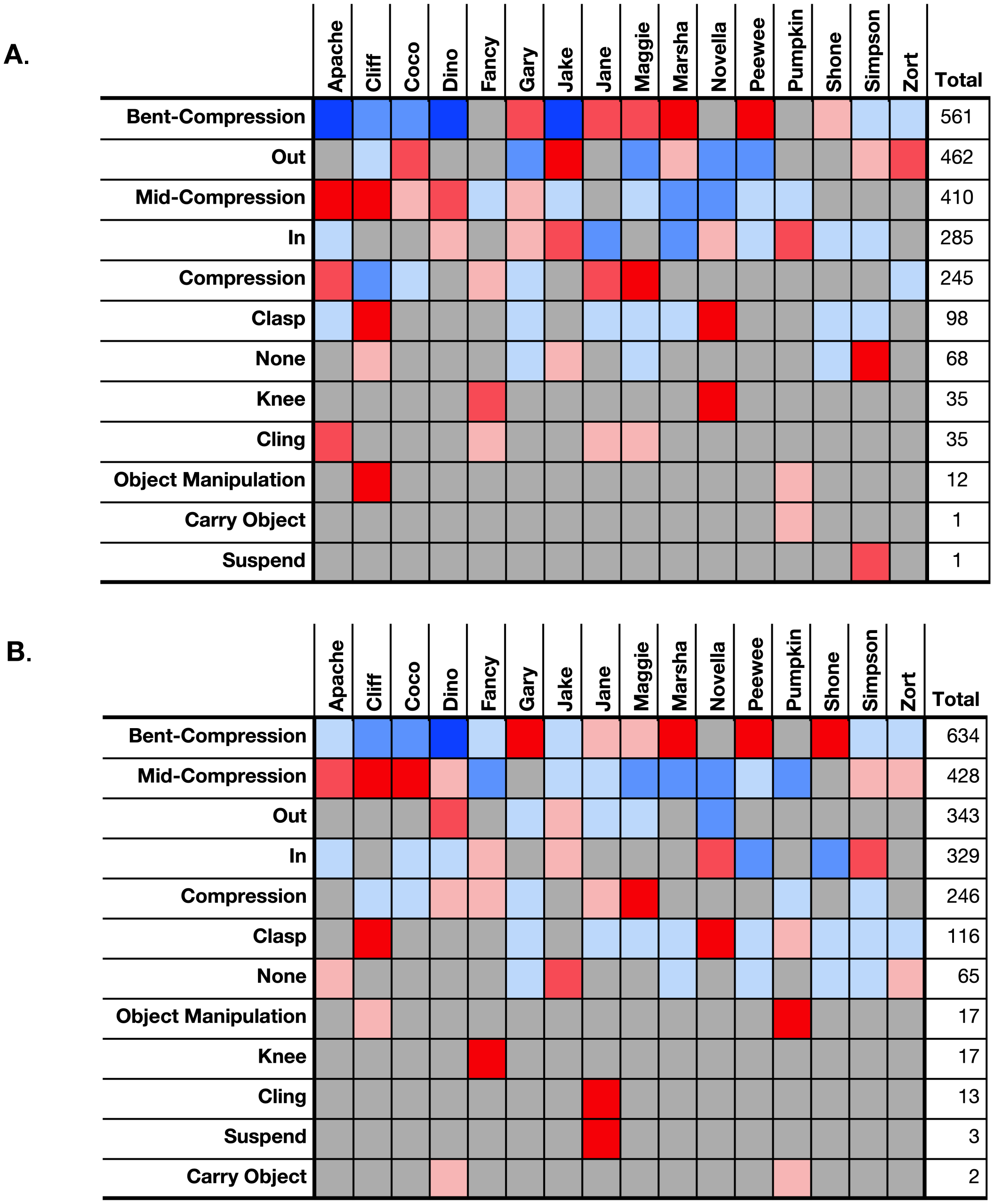
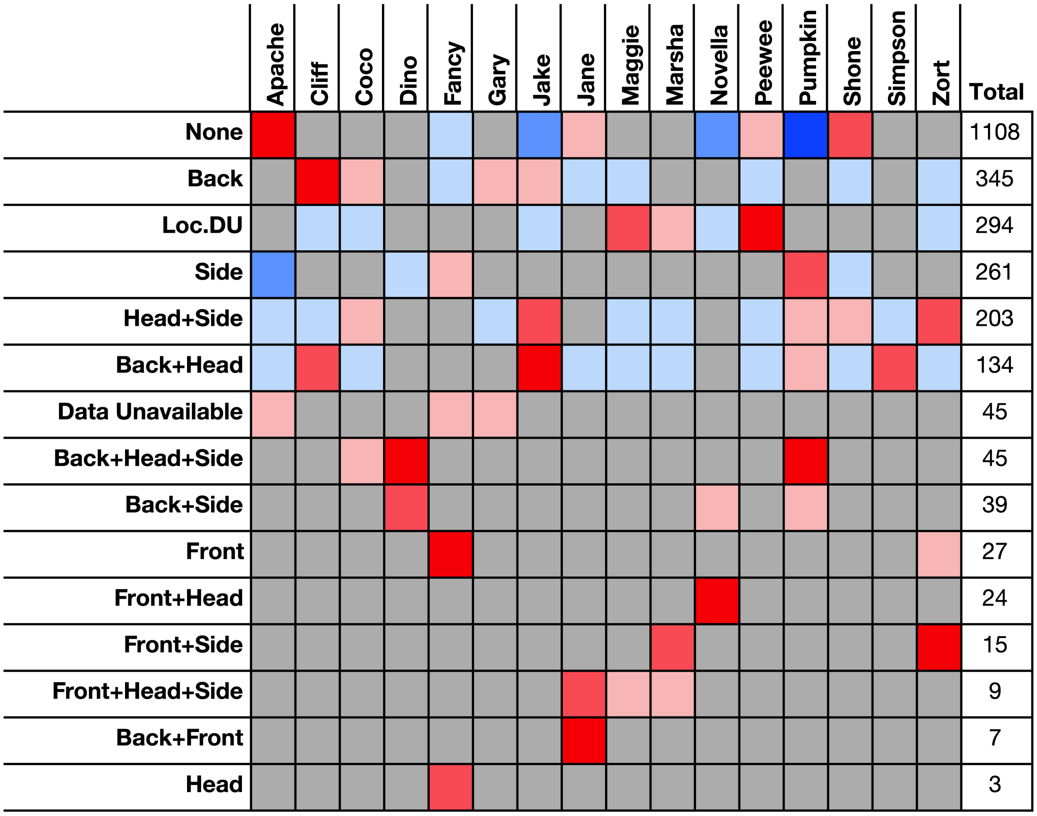
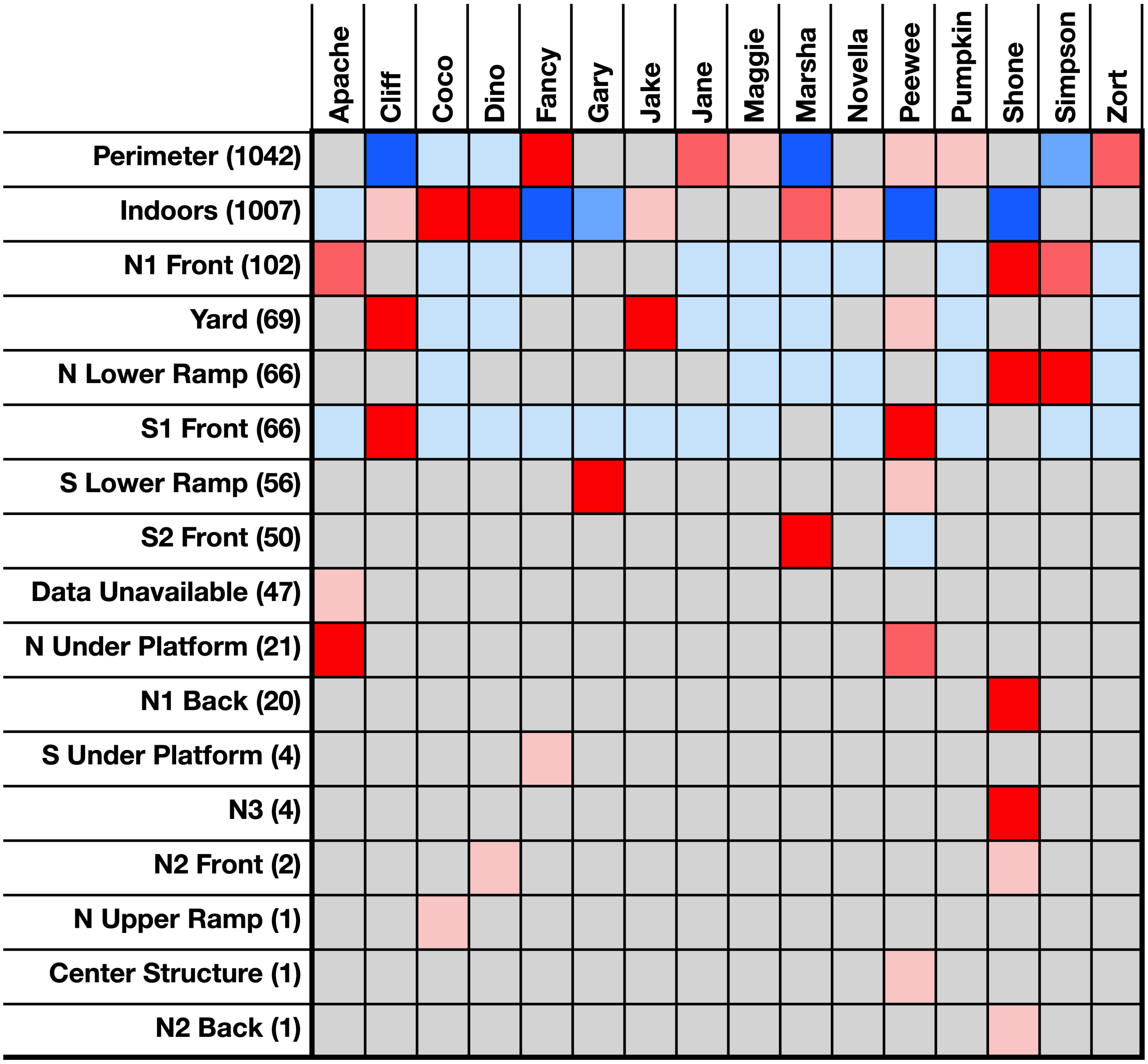


Figure S4.2.2.4 **A**. The differing tendencies for subjects to engage their left leg (Chi-square = 1485.1, df = 165, $p < 2.2 \times 10^{-16}$). **B**. The differing tendencies for subjects to engage their right leg (Chi-square = 1382.5, df = 165, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.



	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort	Total
None																	1108
Back																	345
Loc.DU																	294
Side																	261
Head+Side																	203
Back+Head																	134
Data Unavailable																	45
Back+Head+Side																	45
Back+Side																	39
Front																	27
Front+Head																	24
Front+Side																	15
Front+Head+Side																	9
Back+Front																	7
Head																	3

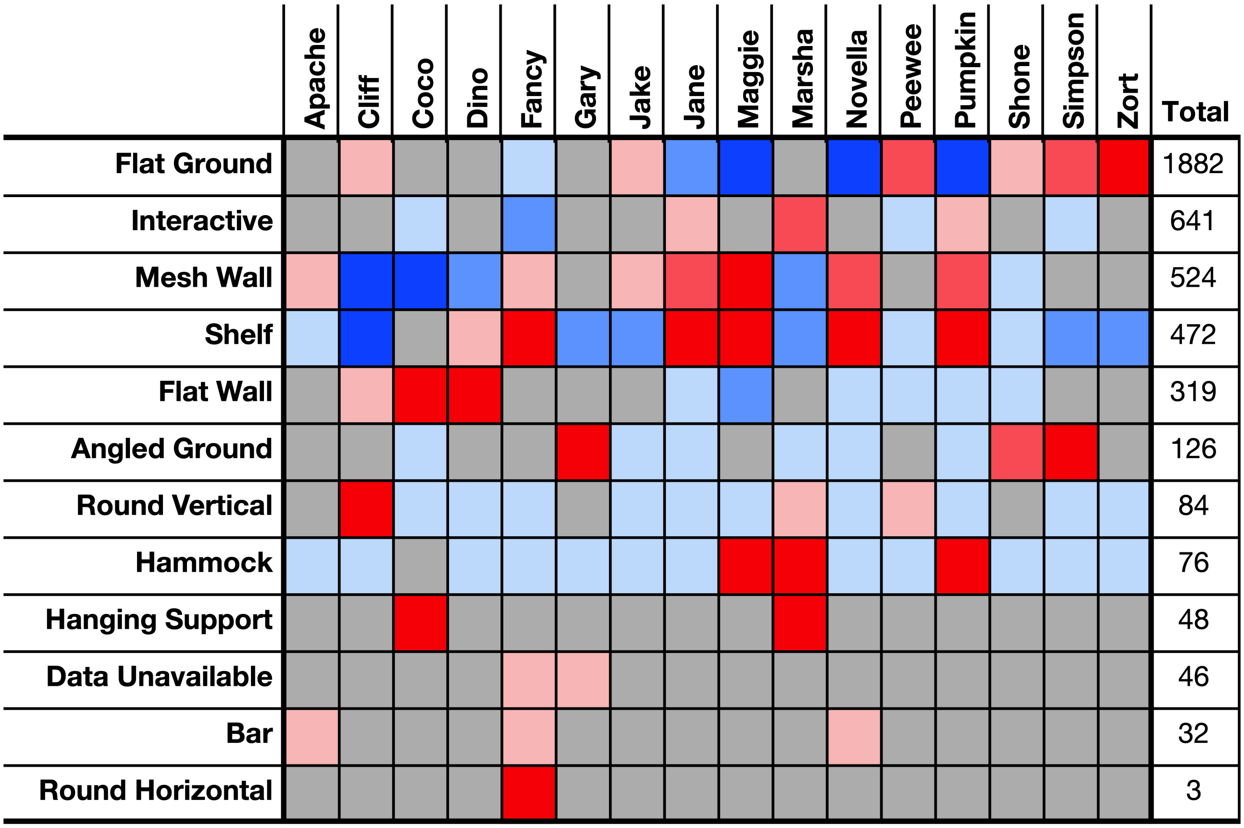
Figure S4.2.2.5 The tendencies for leaning on parts of one's torso were significantly different between subjects (Chi-square = 1382, df = 180, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading. Only the first 20 rows are displayed.



	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort
Perimeter (1042)	⬜	🟦	🩵	🩵	🟥	⬜	⬜	🔴	🩷	🟦	⬜	🩷	🩷	⬜	🔵	🔴
Indoors (1007)	🩵	🩷	🟥	🟥	🟦	🔵	🩷	⬜	⬜	🔴	🩷	🟦	⬜	🟦	⬜	⬜
N1 Front (102)	🔴	⬜	🩵	🩵	🩵	⬜	⬜	🩵	🩵	🩵	🩵	⬜	🩵	🟥	🔴	🩵
Yard (69)	⬜	🟥	🩵	🩵	⬜	⬜	🟥	🩵	🩵	🩵	⬜	🩷	🩵	⬜	⬜	🩵
N Lower Ramp (66)	⬜	⬜	🩵	⬜	⬜	⬜	⬜	⬜	🩵	🩵	🩵	⬜	🩵	🟥	🟥	🩵
S1 Front (66)	🩵	🟥	🩵	🩵	🩵	🩵	🩵	🩵	🩵	⬜	🩵	🟥	🩵	⬜	🩵	🩵
S Lower Ramp (56)	⬜	⬜	⬜	⬜	⬜	🟥	⬜	⬜	⬜	⬜	⬜	🩷	⬜	⬜	⬜	⬜
S2 Front (50)	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟥	⬜	🩵	⬜	⬜	⬜	⬜
Data Unavailable (47)	🩷	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
N Under Platform (21)	🟥	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🔴	⬜	⬜	⬜	⬜
N1 Back (20)	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟥	⬜	⬜
S Under Platform (4)	⬜	⬜	⬜	⬜	🩷	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
N3 (4)	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟥	⬜	⬜
N2 Front (2)	⬜	⬜	⬜	🩷	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🩷	⬜	⬜
N Upper Ramp (1)	⬜	⬜	🩷	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
Center Structure (1)	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🩷	⬜	⬜	⬜	⬜
N2 Back (1)	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🩷	⬜	⬜

Figure S4.3.1.1 Overall occupation of enclosure zones were significantly different between subjects (Chi-square = 295.9, df = 16, $p < 2.2 \times 10^{-16}$). Platform structure zones are split relative to Figure 4.3.1.1. See Figure 4.2.1.1 for description of cell shading. Only enclosure zones that were occupied during the study are reported.

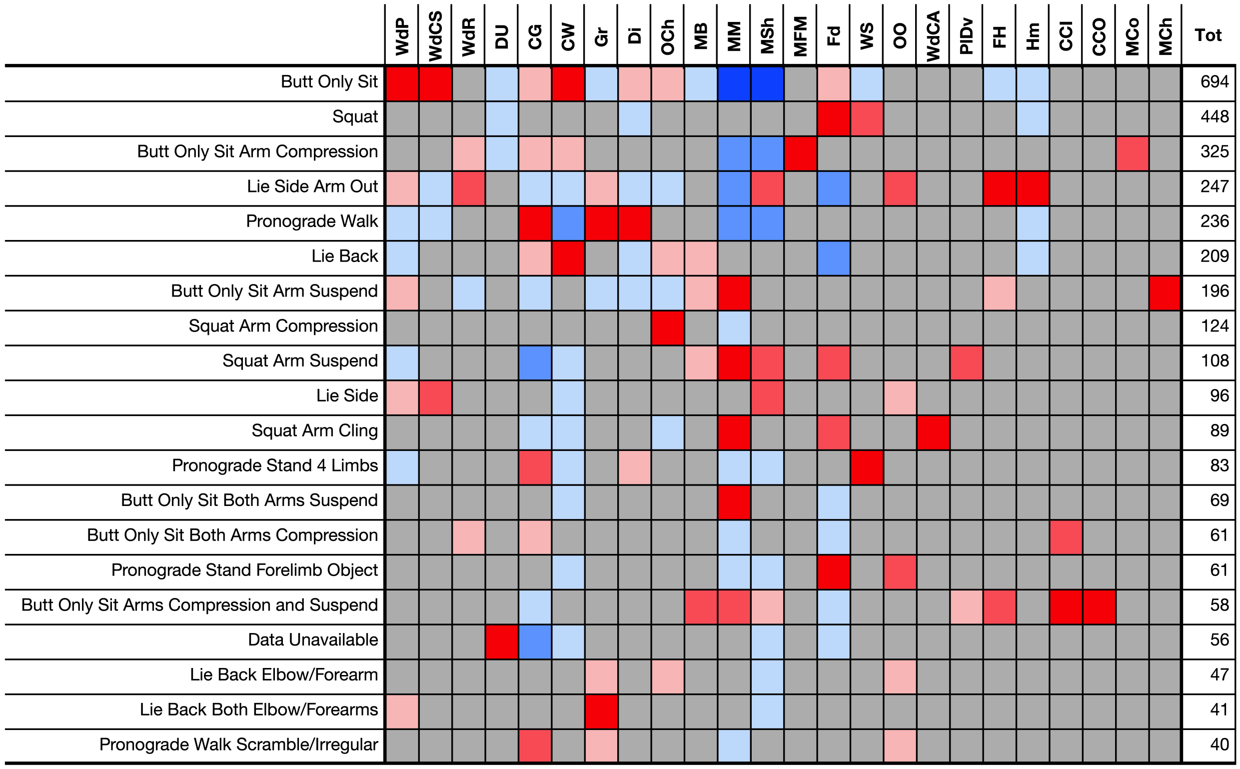
Supplemental Figures S4.3.2



	Apache	Cliff	Coco	Dino	Fancy	Gary	Jake	Jane	Maggie	Marsha	Novella	Peewee	Pumpkin	Shone	Simpson	Zort	Total
Flat Ground	▒	🩷	▒	▒	🩵	▒	🩷	🔵	🟦	▒	🟦	🔴	🟦	🩷	🔴	🟥	1882
Interactive	▒	▒	🩵	▒	🔵	▒	▒	🩷	▒	🔴	▒	🩵	🩷	▒	🩵	▒	641
Mesh Wall	🩷	🟦	🟦	🔵	🩷	▒	🩷	🔴	🟥	🔵	🔴	▒	🔴	🩵	▒	▒	524
Shelf	🩵	🟦	▒	🩷	🟥	🔵	🔵	🟥	🟥	🔵	🟥	🩵	🟥	🩵	🔵	🔵	472
Flat Wall	▒	🩷	🟥	🟥	▒	▒	▒	🩵	🔵	▒	🩵	🩵	🩵	🩵	▒	▒	319
Angled Ground	▒	▒	🩵	▒	▒	🟥	🩵	🩵	▒	🩵	🩵	▒	🩵	🔴	🟥	▒	126
Round Vertical	▒	🟥	🩵	🩵	🩵	▒	🩵	🩵	🩵	🩷	🩵	🩷	🩵	▒	🩵	🩵	84
Hammock	🩵	🩵	▒	🩵	🩵	🩵	🩵	🩵	🟥	🟥	🩵	🩵	🟥	🩵	🩵	🩵	76
Hanging Support	▒	▒	🟥	▒	▒	▒	▒	▒	▒	🟥	▒	▒	▒	▒	▒	▒	48
Data Unavailable	▒	▒	▒	▒	🩷	🩷	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	46
Bar	🩷	▒	▒	▒	🩷	▒	▒	▒	▒	▒	🩷	▒	▒	▒	▒	▒	32
Round Horizontal	▒	▒	▒	▒	🟥	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	3

Figure S4.3.2.1 The differing tendencies for individuals to associate with available substrates in their enclosure, with substrates sorted by their morphological characteristics (Chi-square = 2395.5, df = 165, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

Supplemental Figures S4.4.1



	Tot
Butt Only Sit	694
Squat	448
Butt Only Sit Arm Compression	325
Lie Side Arm Out	247
Pronograde Walk	236
Lie Back	209
Butt Only Sit Arm Suspend	196
Squat Arm Compression	124
Squat Arm Suspend	108
Lie Side	96
Squat Arm Cling	89
Pronograde Stand 4 Limbs	83
Butt Only Sit Both Arms Suspend	69
Butt Only Sit Both Arms Compression	61
Pronograde Stand Forelimb Object	61
Butt Only Sit Arms Compression and Suspend	58
Data Unavailable	56
Lie Back Elbow/Forearm	47
Lie Back Both Elbow/Forearms	41
Pronograde Walk Scramble/Irregular	40

Figure S4.4.1.1 The differing tendencies for positional behaviors under the Pos3 classification schema to be observed when a given subject engages with a defined substrate (Chi-square = 11748, df = 3473, $p < 2.2 \times 10^{-16}$). See Figure 4.2.1.1 for description of cell shading.

Appendix B: Supplemental Tables

Supplemental Tables S4.1.1

Table S4.1.1.1 Change in Proportion of Climbing Events That Include Metal Bar Use and Exclusively Wooden Supports on Either Platform Structure During Both Study Periods.

			Before	Δ	After	Significance
Including Metal Bar	**Ascent Proportion**	**South**	0.00415	=	0.00458	p = 0.675
		North	0.00431	=	0.00398	p = 0.774
	Descent Proportion	**South**	0.00266	=	0.00169	p = 0.134
		North	0.00346	=	0.00274	p = 0.433
Exclusively Wooden Supports	**Ascent Proportion**	**South**	0.00325	>	0.00124	**p = 0.00234**
		North	0.00281	=	0.00147	p = 0.0730
	Descent Proportion	**South**	0.00470	=	0.00409	p = 0.440
		North	0.00325	=	0.00274	p = 0.506

The rates of ascent and descent were calculated as the average occurrences per 30 min trial
See Table 4.1.1 for description of Significance column and cell shading.

Supplemental Tables S4.1.2

Table S4.1.2.1 Combined Occupation Rates of Each Elevation Level.

	Before	Δ	After	Significance
Elevation Level 1	1.1283	>	0.8256	**p = 0.000176**
Elevation Level 2	0.6631	>	0.5231	**p = 0.0397**
Elevation Level 3	0.2059	>	0.1660	**p = 0.0183**
Elevation Level 4	0.0963	=	0.0462	p = 0.1907

See Table 4.1.6 for description of occupation frequency
See Table 4.1.1 for description of Significance column and cell shading.

Table S4.2.1.1 Sex Differences in Expression of Locomotor Versus Postural Behaviors.

	Male	**Female**	**Tot**	**% Tot**	**% M**	**% F**
Posture	3.963 (1434)	-3.963 (779)	2213	86.48	88.52	82.96
Locomotion	-3.231 (161)	3.231 (133)	294	11.49	9.94	14.16
Unsorted	-2.302 (25)	2.302 (27)	52	2.03	1.54	2.88

Male and female subjects expressed postural and locomotor behaviors at significantly different rates (Chi-square = 16.554, df = 2, p = 0.0002543).
See Table 4.2.1.1 for description of cell contents and shading.

Table S4.2.1.2 Sex Differences in Body Orientation.

	Male	**Female**	**Total**	**% Total**	**% Male**	**% Female**
Orthograde	6.609 (969)	-6.609 (435)	1404	54.87	59.81	46.33
Pronograde	-5.985 (626)	5.985 (477)	1103	43.10	38.64	50.80
Unsorted	-2.302 (25)	2.302 (27)	52	2.03	1.54	2.88

Male and female subjects collectively displayed different rates of positioning their bodies in orthograde versus pronograde orientations (Chi-square = 45.287, df = 2, $p < 1.466 \times 10^{-10}$).
See Table 4.2.1.1 for description of cell contents and shading.

Table S4.2.1.3 Sex Differences in Pos7 Behavioral Expression.

	Male	Female	Tot	% Tot	% M	% F
Butt Sit	15.733 (727)	-15.733 (135)	862	33.69	44.88	14.38
Lie Side	-0.784 (205)	0.784 (129)	334	13.05	12.65	13.74
Squat	-5.439 (137)	5.439 (145)	282	11.02	8.46	15.44
Pronograde Walk	-0.995 (130)	0.995 (86)	216	8.44	8.02	9.16
Lie Back	1.799 (143)	-1.799 (64)	207	8.09	8.83	6.82
Side Squat	-6.414 (65)	6.414 (98)	163	6.37	4.01	10.44
Pronograde Stand	-4.947 (51)	4.947 (70)	121	4.73	3.15	7.45
Lie Side and Back	-3.855 (44)	3.855 (54)	98	3.83	2.72	5.75
Unsorted	-2.302 (25)	2.302 (27)	52	2.03	1.54	2.88
Orthograde Stand	-1.721 (27)	1.721 (25)	52	2.03	1.67	2.66
Lie Front	-5.824 (12)	5.824 (38)	50	1.95	0.74	4.05
Pronograde Walk Scramble/Irregular	-3.234 (13)	3.234 (22)	35	1.37	0.80	2.34
Lie on Limbs	0.298 (23)	-0.298 (12)	35	1.37	1.42	1.28
Bipedal	-1.592 (6)	1.592 (8)	14	0.55	0.37	0.85
Arboreal	-3.947 (0)	3.947 (9)	9	0.35	0.00	0.96
Torso-Orthograde Suspensory	-3.255 (1)	3.255 (8)	9	0.35	0.06	0.85
Vertical Descent	-1.525 (2)	1.525 (4)	6	0.23	0.12	0.43
Vertical Climb	-0.677 (3)	0.677 (3)	6	0.23	0.19	0.32
Pronograde Run	1.019 (5)	-1.019 (1)	6	0.23	0.31	0.11
Pronograde Walk Tripedal	-1.314 (0)	1.314 (1)	1	0.04	0.00	0.11
Aerial Leap	0.761 (1)	-0.761 (0)	1	0.04	0.06	0.00

Positional behavior profiles under the Pos7 classification schema were significantly different between male and female subjects (Chi-square = 357.49, df = 20, $p < 2.2 \text{ x}10^{-16}$).
See Table 4.2.1.1 for description of cell contents, shading, and % M and %F columns.
Only the first 20 rows are displayed.

Table S4.2.1.4 Sex Differences in Pos4 Behavioral Expression.

	Male	Female	Tot	% Tot	% M	% F
Lateral Lie	-2.681 (249)	2.681 (183)	432	16.88	15.37	19.49
Squat	-7.141 (190)	7.141 (210)	400	15.63	11.73	22.36
Sit-Out	10.989 (254)	-10.989 (17)	271	10.59	15.68	1.81
Symmetrical Gait Walk	-0.995 (130)	0.995 (86)	216	8.44	8.02	9.16
Chair-Sit	8.975 (193)	-8.975 (17)	210	8.21	11.91	1.81
Back Lie	2.504 (143)	-2.504 (57)	200	7.82	8.83	6.07
Sit/Forelimb Suspend	-0.618 (102)	0.618 (65)	167	6.53	6.30	6.92
Sit-In	3.914 (94)	-3.914 (23)	117	4.57	5.80	2.45
Quadrupedal Stand	-3.663 (46)	3.663 (54)	100	3.91	2.84	5.75
Sit-In/Out	4.904 (79)	-4.904 (11)	90	3.52	4.88	1.17
Supine Lie	-4.305 (35)	4.305 (50)	85	3.32	2.16	5.32
Data Unavailable	-2.302 (25)	2.302 (27)	52	2.03	1.54	2.88
Forelimb Suspend-Squat	-5.145 (12)	5.145 (33)	45	1.76	0.74	3.51
Irregular Gait Pronograde Walk	-3.234 (13)	3.234 (22)	35	1.37	0.80	2.34
Flexed Bipedal Stand	-1.414 (17)	1.414 (16)	33	1.29	1.05	1.70
Stand-Forelimb Suspend	-0.685 (10)	0.685 (8)	18	0.70	0.62	0.85
Flexed Bipedal Walk	-1.592 (6)	1.592 (8)	14	0.55	0.37	0.85
Tripedal Stand	-1.858 (4)	1.858 (7)	11	0.43	0.25	0.75
Orthograde Clamber	-3.255 (1)	3.255 (8)	9	0.35	0.06	0.85
Forelimb Crouch	-3.721 (0)	3.721 (8)	8	0.31	0.00	0.85

Positional behavior profiles under the Pos4 classification schema were significantly different between male and female subjects (Chi-square = 418.19, df = 32, $p < 2.2 \times 10^{-16}$).
See Table 4.2.1.1 for description of cell contents, shading, and % M and %F columns.
Only the first 20 rows are displayed.

Table S4.2.1.5 Sex Differences in Pos3 Behavioral Expression.

	Male	Female	Tot	% Tot	% M	% F
Butt Only Sit	14.367 (385)	-14.367 (21)	406	15.87	23.77	2.24
Squat	-5.648 (109)	5.648 (126)	235	9.18	6.73	13.42
Pronograde Walk	-0.995 (130)	0.995 (86)	216	8.44	8.02	9.16
Lie Side Arm Out	2.404 (139)	-2.404 (56)	195	7.62	8.58	5.96
Butt Only Sit Arm Compression	6.340 (163)	-6.340 (30)	193	7.54	10.06	3.19
Lie Back	-0.799 (70)	0.799 (47)	117	4.57	4.32	5.01
Butt Only Sit Arm Suspend	0.254 (53)	-0.254 (29)	82	3.20	3.27	3.09
Squat Arm Compression	0.675 (47)	-0.675 (23)	70	2.74	2.90	2.45
Lie Side	0.574 (44)	-0.574 (22)	66	2.58	2.72	2.34
Pronograde Stand 4 Limbs	-1.974 (33)	1.974 (31)	64	2.50	2.04	3.30
Data Unavailable	-2.302 (25)	2.302 (27)	52	2.03	1.54	2.88
Butt Only Sit Both Arms Compression	3.050 (39)	-3.050 (7)	46	1.80	2.41	0.75
Squat Arm Suspend	-4.709 (12)	4.709 (30)	42	1.64	0.74	3.19
Squat Arm Cling	-3.238 (14)	3.238 (23)	37	1.45	0.86	2.45
Pronograde Walk Scramble/Irregular	-3.234 (13)	3.234 (22)	35	1.37	0.80	2.34
Butt Only Sit Both Arms Suspend	1.494 (25)	-1.494 (8)	33	1.29	1.54	0.85
Pronograde Stand Forelimb Object	-4.401 (7)	4.401 (22)	29	1.13	0.43	2.34
Butt Only Sit Arms Compression and Suspend	-2.233 (11)	2.233 (15)	26	1.02	0.68	1.60
Lie Back Elbow/Forearm	3.084 (24)	-3.084 (2)	26	1.02	1.48	0.21
Squat Both Arms Compression	-1.784 (11)	1.784 (13)	24	0.94	0.68	1.38

Positional behavior profiles under the Pos3 classification schema were significantly different between male and female subjects (Chi-square = 791.03, df = 151, p < 2.2 x10^{-16}).
See Table 4.2.1.1 for description of cell contents, shading, and % M and %F columns.
Only the first 20 rows are displayed.

Table S4.2.1.6 Differences in Pos3 Behavioral Expression by Study Period.

	Before	After	Tot	% Tot	% Before	% After
Butt Sit	1.854 (453)	-1.854 (409)	862	33.69	35.42	31.95
Lie Side	-2.340 (147)	2.340 (187)	334	13.05	11.49	14.61
Squat	0.133 (142)	-0.133 (140)	282	11.02	11.10	10.94
Pronograde Walk	-1.701 (96)	1.701 (120)	216	8.44	7.51	9.38
Lie Back	1.818 (116)	-1.818 (91)	207	8.09	9.07	7.11
Side Squat	-1.371 (73)	1.371 (90)	163	6.37	5.71	7.03
Pronograde Stand	0.098 (61)	-0.098 (60)	121	4.73	4.77	4.69
Lie Side and Back	1.034 (54)	-1.034 (44)	98	3.83	4.22	3.44
Unsorted	4.766 (43)	-4.766 (9)	52	2.03	3.36	0.70
Orthograde Stand	1.964 (33)	-1.964 (19)	52	2.03	2.58	1.48
Lie Front	-1.140 (21)	1.140 (29)	50	1.95	1.64	2.27
Pronograde Walk Scramble/Irregular	0.173 (18)	-0.173 (17)	35	1.37	1.41	1.33
Lie on Limbs	-5.614 (1)	5.614 (34)	35	1.37	0.08	2.66
Bipedal	-2.142 (3)	2.142 (11)	14	0.55	0.23	0.86
Arboreal	-1.001 (3)	1.001 (6)	9	0.35	0.23	0.47
Torso-Orthograde Suspensory	-1.001 (3)	1.001 (6)	9	0.35	0.23	0.47
Pronograde Run	0.818 (4)	-0.818 (2)	6	0.23	0.31	0.16
Vertical Climb	-0.816 (2)	0.816 (4)	6	0.23	0.16	0.31
Vertical Descent	1.636 (5)	-1.636 (1)	6	0.23	0.39	0.08
Aerial Leap	-1.000 (0)	1.000 (1)	1	0.04	0.00	0.08
Pronograde Walk Tripedal	1.001 (1)	-1.001 (0)	1	0.04	0.08	0.00

Collective positional behavior expressions under the Pos3 classification schema were significantly different between study periods (Chi-square = 398.41, df = 151, $p < 2.2 \times 10^{-16}$).
See Table 4.2.1.1 for description of cell contents, and shading.
Only the first 20 rows are displayed.

Table S4.2.1.7 Difference in Group Expression of Locomotor Versus Postural Behaviors by Study Period.

	Before	After	Total	% Total	% Before	% After
Posture	1.608 (1104)	-1.608 (1109)	2213	88.27	89.32	87.25
Locomotion	-1.608(132)	1.608 (162)	294	11.73	10.68	12.75

Overall tendencies to engage in locomotion versus stationary postures were not significantly different between the periods before and after the installation of the climbing aid (Chi-square = 2.5844, df = 1, p = 0.1079).
See Table 4.2.1.1 for description of cell contents and shading.

Table S4.2.3.1 Individual Diversity and Evenness Indices for the Engagement of Each Limb.

	Right Arm		Left Arm		Right Leg		Left Leg	
	H	**J**	**H**	**J**	**H**	**J**	**H**	**J**
Apache	**1.91**	0.87	**2.02**	0.88	**1.72**	0.88	**1.53**	0.73
Cliff	**1.57**	0.71	**1.72**	0.75	**1.68**	0.81	**1.70**	0.82
Coco	**1.79**	0.86	**1.77**	0.81	**1.61**	0.77	**1.61**	0.77
Dino	**1.96**	0.85	**1.89**	0.82	**1.63**	0.78	**1.58**	0.88
Fancy	**2.04**	0.89	**2.19**	0.91	**1.95**	0.89	**2.04**	0.93
Gary	**1.64**	0.71	**1.94**	0.81	**1.25**	0.78	**1.31**	0.81
Jake	**1.90**	0.82	**2.01**	0.87	**1.85**	0.89	**1.70**	0.77
Jane	**1.94**	0.88	**2.02**	0.88	**1.68**	0.81	**1.48**	0.76
Maggie	**2.00**	0.87	**1.88**	0.90	**1.30**	0.73	**1.43**	0.80
Marsha	**2.12**	0.97	**1.80**	0.82	**1.28**	0.79	**1.02**	0.63
Novella	**1.70**	0.78	**1.68**	0.76	**1.57**	0.71	**1.86**	0.85
Peewee	**1.90**	0.86	**1.55**	0.87	**1.13**	0.58	**1.20**	0.57
Pumpkin	**2.03**	0.85	**2.09**	0.87	**1.95**	0.85	**1.89**	0.82
Shone	**1.97**	0.86	**1.97**	0.90	**1.28**	0.80	**1.50**	0.77
Simpson	**2.05**	0.86	**2.17**	0.90	**1.47**	0.91	**1.69**	0.87
Zort	**1.93**	0.84	**1.95**	0.85	**1.74**	0.84	**1.61**	0.77
Mean	**1.90**	0.84	**1.92**	0.85	**1.57**	0.80	**1.57**	0.79

Shannon diversity index (H) and species evenness (J) calculated for each individual based on their rates of limb engagement expression for each arm and each leg.
See Table 4.2.3.1 for description of cell shading and text coloring.

Table S4.2.3.2 Individual Diversity and Evenness Indices for Pooled Arm, Leg, and Limb Engagement.

	Any Arm		Any Leg		Any Limb	
	H	J	H	J	H	J
Apache	2.66	0.90	2.32	0.85	3.18	0.90
Cliff	2.34	0.79	2.38	0.86	3.05	0.86
Coco	2.48	0.87	2.30	0.83	3.08	0.88
Dino	2.62	0.88	2.30	0.87	3.15	0.89
Fancy	2.81	0.92	2.69	0.93	3.44	0.94
Gary	2.48	0.82	1.97	0.86	2.92	0.85
Jake	2.65	0.88	2.47	0.87	3.25	0.90
Jane	2.67	0.91	2.27	0.84	3.17	0.90
Maggie	2.63	0.91	2.06	0.83	3.04	0.89
Marsha	2.66	0.92	1.84	0.80	2.94	0.88
Novella	2.38	0.82	2.41	0.83	3.09	0.86
Peewee	2.42	0.89	1.86	0.69	2.83	0.83
Pumpkin	2.75	0.89	2.61	0.87	3.37	0.90
Shone	2.66	0.90	2.09	0.84	3.07	0.89
Simpson	2.80	0.91	2.27	0.92	3.23	0.92
Zort	2.63	0.88	2.37	0.86	3.19	0.89
Mean	2.60	0.88	2.26	0.85	3.13	0.89

Shannon diversity index (H) and species evenness (J) calculated according to each individual's rates of limb engagements. The overarching columns represent the the pooled engagement of any arm, the pooled engagement of any leg, and the combined engagement of all four limbs.

See Table 4.2.3.1 for description of cell shading and text coloring.

Table S4.2.3.3 Individual Diversity and Evenness Indices for Limb Use Combinations.

	Ipsilateral		Contralateral		Both Arms		Both Legs	
	H	J	H	J	H	J	H	J
Apache	3.24	0.88	3.34	0.85	2.98	0.89	2.72	0.87
Cliff	2.88	0.80	2.86	0.81	2.48	0.79	2.48	0.81
Coco	3.04	0.82	3.14	0.86	2.47	0.81	2.65	0.89
Dino	3.15	0.87	3.11	0.85	2.84	0.91	2.52	0.89
Fancy	3.41	0.90	3.49	0.88	3.01	0.85	2.86	0.90
Gary	2.85	0.81	2.92	0.82	2.77	0.86	2.17	0.80
Jake	3.49	0.90	3.47	0.90	2.87	0.88	2.81	0.86
Jane	3.13	0.87	3.22	0.87	3.04	0.91	2.34	0.84
Maggie	2.96	0.85	2.98	0.84	2.84	0.89	2.20	0.78
Marsha	2.69	0.82	2.74	0.85	2.73	0.90	1.80	0.87
Novella	3.08	0.81	3.01	0.83	2.53	0.78	2.43	0.83
Peewee	2.83	0.81	2.80	0.79	2.68	0.84	1.99	0.69
Pumpkin	3.55	0.88	3.55	0.88	3.22	0.87	2.86	0.85
Shone	2.81	0.82	2.94	0.83	2.90	0.89	2.25	0.83
Simpson	3.21	0.90	3.28	0.90	2.90	0.86	2.43	0.84
Zort	3.30	0.87	3.30	0.88	2.73	0.85	2.68	0.89
Mean	3.10	0.85	3.13	0.85	2.81	0.86	2.45	0.84

Shannon diversity index (H) and species evenness (J) calculated according to each individual's rates of limb engagement combinations. The overarching columns represent the pooled simultaneous engagement of ipsilateral limbs, the pooled simultaneous engagement of contralateral limbs, the simultaneous engagement of both arms, and the simultaneous engagements of both legs.

See Table 4.2.3.1 for description of cell shading and text coloring.

Supplemental Tables S4.3.1

Table S4.3.1.1 Enclosure Zone Occupation Differences by Sex

	Male	Female	Total	% Total	% Male	% Female
Perimeter	-6.065 (587)	6.065 (455)	1042	40.7	36.2	48.5
Indoors	-1.720 (617)	1.720 (390)	1007	39.4	38.1	41.5
N1 Front	7.637 (101)	-7.637 (1)	102	4.0	6.2	0.1
Yard	5.398 (65)	-5.398 (4)	69	2.7	4.0	0.4
S1 Front	5.231 (62)	-5.231 (4)	66	2.6	3.8	0.4
N Lower Ramp	4.714 (60)	-4.714 (6)	66	2.6	3.7	0.6
S Lower Ramp	4.639 (52)	-4.639 (4)	56	2.2	3.2	0.4
S2 Front	-9.380 (0)	9.380 (50)	50	2.0	0.0	5.3
Data Unavailable	-1.758 (24)	1.758 (23)	47	1.8	1.5	2.4
N Under Platform	3.503 (21)	-3.503 (0)	21	0.8	1.3	0.0
N1 Back	3.418 (20)	-3.418 (0)	20	0.8	1.2	0.0
S Under Platform	-0.553 (2)	0.553 (2)	4	0.2	0.1	0.2
N3	1.524 (4)	-1.524 (0)	4	0.2	0.2	0.0
N2 Front	1.077 (2)	-1.077 (0)	2	0.1	0.1	0.0
N Upper Ramp	0.761 (1)	-0.761 (0)	1	0.0	0.1	0.0
Center Structure	0.761 (1)	-0.761 (0)	1	0.0	0.1	0.0
N2 Back	0.761 (1)	-0.761 (0)	1	0.0	0.1	0.0

Overall occupation rates of enclosure zones were significantly different between male and female subjects (Chi-square = 295.9, df = 16, $p < 2.2 \text{ x}10^{-16}$).
Platform structure zones are split relative to Table 4.3.1.1.
See Table 4.2.1.1 for description of cell contents, and shading.

Table S4.3.1.2 Enclosure Zone Occupation Differences Between Study Periods

	Before	After	Total	% Total	% Before	% After
Perimeter (1042)	-2.08 (495)	2.08 (547)	1042	40.7	38.7	42.7
Indoors (1007)	-2.29 (475)	2.29 (532)	1007	39.4	37.1	41.6
N1 Front (102)	-0.60 (48)	0.60 (54)	102	4.0	3.8	4.2
Yard (69)	3.54 (49)	-3.54 (20)	69	2.7	3.8	1.6
S1 Front (66)	3.99 (49)	-3.99 (17)	66	2.6	3.8	1.3
N Lower Ramp (66)	-1.24 (28)	1.24 (38)	66	2.6	2.2	3.0
S Lower Ramp (56)	-0.54 (26)	0.54 (30)	56	2.2	2.0	2.3
S2 Front (50)	-0.85 (22)	0.85 (28)	50	2.0	1.7	2.2
Data Unavailable (47)	5.45 (42)	-5.45 (5)	47	1.8	3.3	0.4
N Under Platform (21)	3.29 (18)	-3.29 (3)	21	0.8	1.4	0.2
N1 Back (20)	4.49 (20)	-4.49 (0)	20	0.8	1.6	0.0
S Under Platform (4)	-1.00 (1)	1.00 (3)	4	0.2	0.1	0.2
N3 (4)	2.00 (4)	-2.00 (0)	4	0.2	0.3	0.0
N2 Front (2)	-1.41 (0)	1.41 (2)	2	0.1	0.0	0.2
N Upper Ramp (1)	1.00 (1)	-1.00 (0)	1	0.0	0.1	0.0
Center Structure (1)	1.00 (1)	-1.00 (0)	1	0.0	0.1	0.0
N2 Back (1)	-1.00 (0)	1.00 (1)	1	0.0	0.0	0.1

Overall occupation of enclosure zones were significantly different between the periods before and after the climbing aid's installation (Chi-square = 106.24, df = 16, p = 2.315 x10^{-15}).
Platform structure zones are split relative to Table 4.2.1.5.
See Table 4.2.1.1 for description of cell contents, and shading.

Table S4.3.1.3 Sunlight Exposure Category Differences Between Study Periods

	Before	After	Total	% Total	% Before	% After
In Shade	1.54 (553)	-1.54 (515)	1068	41.74	43.24	40.23
Indoors	-2.29 (475)	2.29 (532)	1007	39.35	37.14	41.56
Partial Shade	-1.06 (100)	1.06 (115)	215	8.40	7.82	8.98
In Light	-1.01 (82)	1.01 (95)	177	6.92	6.41	7.42
Data Unavailable	4.89 (69)	-4.89 (23)	92	3.60	5.39	1.80

Rates of inhabiting different sunlight exposure categories before and after the installation of the climbing aid were significantly different (Chi-square = 29.579, df = 4, p = 5.961 x10^{-6}).
See Table 4.2.1.1 for description of cell contents, and shading.

Supplemental Tables S4.4.2

Table S4.4.2.1 Positional Diversity by Substrate Combination

	Pos1	
	H	J
Metal Shelf+Metal Mesh	4.32	0.93
Concrete Ground	4.05	0.87
Concrete Ground+Metal Mesh	4.03	0.93
Metal Shelf	3.65	0.89
Concrete Ground+Concrete Wall	3.48	0.83
Wood Ramp	3.22	0.93
Concrete Ground+Other Chimp	3.18	0.83
Wood Platform	3.16	0.90
Hammock	3.07	0.89
Concrete Ground+Food	2.92	0.91
Concrete Ground+Metal Mesh+Food	2.86	0.96
Concrete Ground+Other Object	2.81	0.92
Concrete Ground+Metal Mesh+Other Object	2.63	0.97
Metal Shelf+Metal Mesh+Food	2.55	0.94
Concrete Ground+Metal Mesh+Water Spout	2.52	0.98
Wood Platform+Wood Column (Side)	2.52	0.87
Wood Platform+Other Chimp	2.30	1.00
Grass	2.26	0.91
Metal Shelf+Metal Mesh+Other Chimp	2.21	0.96
Concrete Ground+Wood Ramp	2.20	0.92
Concrete Ground+Concrete Wall+Food	2.15	0.94
Metal Shelf+Other Chimp	2.10	0.91
Dirt	2.04	0.82
Concrete Ground+Water Spout	1.82	0.88
Concrete Ground+Metal Bar	1.79	1.00
	2.79	0.92

Shannon diversity index (H) and species evenness (J) calculated for each substrate combination based on their rates of expression of positional behaviors in accordance with the Pos1 classification schema.
See Table 4.2.3.1 for description of cell shading and text coloring.
Only the first 20 rows are displayed.