EFFECTS OF NATURAL VS NON-NATURAL ENRICHMENT ITEMS ON CAPTIVE ORANGUTAN BEHAVIOR

A THESIS

SUBMITTED TO THE GRADUATE SCHOOL

IN PARTIAL FULFULLMENT OF THE REQUIREMENTS

FOR A MASTER OF SCIENCE DEGREE

BY:

KAYLIN CROSBY

DEPARTMENT OF BIOLOGY

BALL STATE UNIVERSITY

MUNCIE, INDIANA

ADVISOR: DR. GARY DODSON

JULY 2015

ACKNOWLEDGMENTS

I would like to whole heartedly thank those individuals who have helped and encouraged me during this process. Your support gave me the power and determination to complete my thesis, and for that I am forever grateful.

First and foremost, I thank my advisor Dr. Gary Dodson. I could not have asked for a better mentor during this process. He has given me impeccable insight into the field of animal behavior and has helped the past two years become the most educational and rewarding of my life. I am extremely grateful for his guidance and cannot thank him enough.

My sincere thanks and appreciation goes out to the Fort Wayne Children's Zoo and the Louisville Zoo for allowing me to conduct my study at their institutions. The keepers and other personnel at both zoos were nothing but accommodating to the needs of the study. I thank them for taking time out of their busy schedules to make this project the best it could be.

I also extend thanks to my committee members Dr. Timothy Carter and Dr. Kamal Islam whose time, support, and contributions have undoubtedly helped to ease the stress and frustration associated with this project. I would like to send out a special thank you to Jason Doll for helping me with statistics. His patience was greatly appreciated.

Next, I am extremely appreciative of those who put in countless hours of data collection and organization: Aisyah Aziz, Samantha Brown, Erica Doyle, Abby Fink, Alexandra Loughmiller, Levi Smith, Holly Walsh, and Carrie Wilson. Because of their time and dedication, we were able to successfully and efficiently complete this project. Thank you.

I am also exceptionally grateful for my loving friends and family. My parents, Jerry and Rhonda Crosby, have always supported me in whatever endeavor I pursue. Their constant encouragement has allowed me to become the woman that I am today. My amazing fiancé, Jonathan Tennant, has shown

me nothing but love and support through this entire, and at times stressful, process. I thank him for understanding the amount of time it takes to successfully complete such a project.

Finally, I would like to thank those individuals who helped me discover my true passion for animal behavior and captive great ape welfare, including Dr. Collette Thogerson, Dr. Joseph Garner, Dr. Stephen Ross, and Dr. Robert Shumaker. Without them, I would not be on this incredible journey.

Funding for this project was provided by the Ball State University chapter of Sigma Xi, Ball State's ASPIRE internal grant program, and Ball State University's Department of Biology. I graciously thank them for their financial contributions.

TABLE OF CONTENTS

CHAPTER 1:

LITERATURE REVIEW

There are currently two recognized species of orangutan: the Sumatran orangutan (*Pongo abelii*) and the Bornean orangutan (*Pongo pygmaeus*) [Groves, 1999; Muir et al., 2000; Zhang et al., 2001]. Based on mitochondrial DNA classification, *Pongo pygmaeus* has been further divided into three subspecies: the Northeast Bornean orangutan (*P.p. morio) (Northeast Borneo)*, the Northwest Bornean orangutan *(P.p. pygmaeus)*, and the Central Bornean orangutan (*P.p. wurmbii)* [Groves, 1999]. This division is based largely on geographic range [Taylor & van Schaik, 2007; van Schaik et al., 2009; Wich et al., 2012].

P. abelii and *P. pygmaeus* are very similar, both morphologically and behaviorally; however subtle differences exist [Groves, 2001; Rowe, 1996; van Schaik et al., 2009]. Overall, *P. abelii* have a thinner body shape with longer, lighter hair compared to *P. pygmaeus* [Courtenay et al. 1988; Groves 2001]. *P. abelii* also has a greater average brain size at 388cc compared to 369cc of *P. pygmaeus* [Taylor and van Schaik, 2007]. Both species are sexually dimorphic with males weighing around 90 kg and females around 45 kg [Markham & Groves 1990; Rodman, 1984]; average weights for captive orangutans are higher [Cocks, 1998, 2007; MacKinnon, 1971]. Some males develop facial secondary sex characteristics with age [Winkler, 1989]. These prominent cheek pads, or flanges, are usually accompanied with vast, throat sacs, both of which are larger in *P. pygmaeus* [Kuze et al., 2005; Masterson and Leutenegger, 1992; Rowe, 1996]. Behaviorally, *P. pygmaeus* reside in smaller social groups and travel terrestrially at higher frequencies than *P. abelii* [Loken et al., 2013; Mitra Setia et al., 2009; van Schaik et al., 2009].

The populations of both *P. pygmaeus* and *P. abelii* are in continual decline [Rijksen and Meijaard 1999; van Schaik et al., 2001]. Currently, the IUCN Red List classifies *P. pygmaeus* as endangered [Ancenaz et al., 2008] and *P. abelii* as critically endangered [Singleton et al., 2008]. Estimates for wild orangutan populations are approximate due to inaccessibility and poor forest visibility [Rijksen and Meijaard 1999; Sodaro 2007]. However, in 2003 an estimated 55,000 *P. pygmaeus* individuals were residing in the 86,000km^2 sustainable habitat remaining in Borneo, while approximately 7,000 *P. abelii* individuals were living in a mere 8,992km^2 of suitable land in Northern Sumatra [Singleton et al., 2004]. A more recent study reexamined the remaining population and provided the estimates for subspecies: approximately 6,624 *P. abelii;* 3,143-4,261 *P.p. pygmaeus;* 35,000 *P.p. wurmbii*; 15,842 *P.p. morio* [Wich et al., 2008]. Orangutan populations are expected to decline continuously throughout the next two decades, due mainly to habitat destruction [Singleton et al, 2004; Yeager, 1999]. Thus, both species are subject to extinction in the near future if rates of habitat destruction are not reduced [Morrogh-Bernard et al. 2003].

Orangutan Activity Budgets

An animal's activity budget can be defined as the total amount of time, usually expressed in percentages, which an animal devotes to various activities each day [Bean, 1998; Williamson and Dunbar, 1999]. In the wild, orangutan activity budgets comprise mostly eating, resting, and traveling [Kanamori et al., 2010; Morrogh-Bernard et al., 2009; Rodman, 1988]. Although daily percentages of time spent in each activity vary between age groups, geographic locations, and seasons [Fox et al., 2004; Mitani, 1989; Morrogh-Bernard, 2009; Wich et al. 2006], on average wild orangutans spend around 50-60% of their waking time foraging and consuming food, around 25-35% resting, and around 10-15% traveling [Galdikas, 1988; Knott, 1998; Mitani, 1989; Morrogh-Bernard et al., 2009; Rodman, 1979].

The diet of wild orangutans is diverse and seasonally dependent [Bastian et al., 2010; Knott, 1998; Morrogh-Bernard, 2009; Wich et al., 2006]. However, fruit is the leading food source, at times

making up 50-100% of their diet [Kanamori et al., 2010; Knott, 1998a; Morrogh-Bernard, 2009; van Schaik and van Hooff, 1996]. Sumatra experiences a longer fruiting season than Borneo; thus fruit is always a major food item for *Pongo abelii* [Wich et al., 2006]. During Borneo's wet season, when fruit is scarce, *Pongo pygmaeus* rely on other significant sources for caloric intake: leaves, bark, and invertebrates [Morrogh-Bernard, 2009; Rodman, 1988].

There are two feeding strategies for orangutans, the 'sit and wait' method and the 'search and find' method. The utilization of these methods is dependent upon location and habitat [Morrogh-Bernard, 2009]. Orangutans in Sumatra or those in Borneo during dry season have plenty of food available to them, thus they are able to actively travel to 'search and find' their food. During low fruiting season in Borneo, orangutans employ the 'sit and wait' strategy, during which they feed on large quantities of lower quality foods while traveling slowly to conserve as much energy as possible until fruit availability increases. Thus, orangutans are more active during periods of high fruiting [Morrogh-Bernard, 2009].

Food availability also seems to impact social structure and group size of wild orangutans [Knott, 1998b, Wich et al., 2006]. Although these apes are primarily believed to be semi-solitary primates, with the only true social groups being those of mothers and offspring [Galdikas 1984; te Boekhorst et al. 1990], they have also been known to form groups when food is readily abundant [Knott, 1998b; Mitani et al., 1991; Utami et al., 1997; van Schaik, 1999]. Wich et al. (2006) hypothesized that this was the reason for larger group sizes in Sumatra relative to Borneo. In the areas that promote larger parties, there are two predominant types of social groups: travel bands and feeding aggregations [Utami et al., 1997]. Travel bands are assemblages of a few individuals that travel together between feeding sites [Delgado and van Schaik, 2000; van Schaik and van Hooff, 1996]. Feeding aggregations are larger groups that form in fruiting trees. The greater amount of available food in one location decreases competition and allows for affiliative interactions [van Schaik and van Hooff, 1996; van Schaik et al., 2004]. Such

outcomes suggest that if appropriate quantities of fruit were consistently available, permanent social groups of orangutan could be prevalent [Delgado and van Schaik, 2000].

The provision of ample diets to orangutans in captive settings precludes the need to forage or compete for their necessary caloric intake, and their social structures in captivity reflect this. Instead of being primarily semi-solitary, the social structure of captive orangutans more closely mirrors that of wild orangutans in areas of plentiful food, and they easily form enduring social connections [Edwards and Snowden, 1980; Perkins, 1992]. Captive males and females of all ages can form inter- and intra-sexual relationships, though adult, flanged males prefer to keep their distance from each other [Poole, 1987; Tobach et al., 1989; Zucker et al., 1986].

The provisioned diet may also impact their daily activity levels and health [Knott, 1998a]. Captive orangutans do not need to spend time actively foraging or traveling for food. With only 10%-20% of their time spent feeding [Hebert and Bard, 2000; Pizzutto et al., 2008], they have more time to dedicate to other activities. This extra time usually leads to increased frequencies of inactivity, especially in unenriched environments [Perkins, 1992; Pizzutto et al., 2008]. Idleness is common for captive orangutans [Wright, 1995], with individuals spending up to 70% of their time inactive [Hebert and Bard, 2000; Perkins, 1992; Pizzutto et al., 2008]. Also, the suggestion that orangutans are well adapted for fat storage because of their need to survive the fluctuating availabilities of fruit in their habitat [Leighton, 1993; Mackinnon, 1974] might explain the predominance of obesity-associated diseases in captive orangutans relative to other apes [Mackinnon, 1971; Maple, 1980]. Knott [1998a] states that wild orangutans often binge on fruit when it is available and store the excess energy for a future time when food becomes less abundant. Their tendency to overindulge on available food, their ability to store fat efficiently, and their low levels of activity are all contributing factors to the obesity of captive orangutans [Knott, 1998a].

Zoo Exhibits

Zoo enclosures have gone through multiple major transformations since their European rise over 200 years ago [Moss et al., 2010; Shettel-Neuber, 1988]. These transformations are usually broken down into the categories of first, second, and third generation exhibits [Campbell, 1984; Coe and Maple, 1984; Moss, 2010; Shettel-Neuber, 1988]. First generation exhibits, popular in the eighteenth century, are no longer prevalent. These enclosures were composed of small, barren, barred cages clustered tightly together in exhibit arenas [Shettel-Neuber, 1988]. Second generation exhibits became popular in the mid-20th century. They were constructed using cement as the lower foundation and employed large moats or valleys, instead of bars, as a means of confinement. Finally, third generation exhibits encompass more elements of the animals' natural environment [Coe, 1985; Coe and Maple, 1984; Moss et al., 2010; Shettel-Neuber, 1988]. Such enclosures are constructed with the animals' natural history in mind and usually allow adequate space to house more species-specific social groupings of the animals [Chang et al., 1999]. These exhibits also have much more vegetation and natural appearing landscapes. Today, American zoos still employ some second generation exhibits, but many are striving to renovate such enclosures to meet the naturalistic standards of third generation exhibits [Chang et al., 1999; Lukas and Ross, 2014; Maple and Stine, 1982; Moss et al., 2010; Shettel-Neuber, 1988].

The current focus on the importance of naturalistic enclosures stems from two main goals: to improve the well-being of the confined animals and to increase the educational and recreational benefits to visitors [Gold, 1997; Maple, 1983; Price et al., 1994]. Some researchers maintain that naturalistic environments increase the exhibition of natural behaviors in captive animals [Campbell, 1984; Newberry, 1995]. Research has shown that the transition from a barren cage to more naturalistic environments has caused a decrease in stereotypic and aggressive behaviors, as well as an increase in affiliative behaviors and overall activity [Chang et al., 1999; Clarke et al., 1982; Coe, 1985; Ogden et al., 1990, O'Neill et al., 1991; Maple and Stine, 1982; Maple and Finlay, 1986]. However, the variable of

increased size was also associated with these newer, naturalistic enclosures, so it is difficult to determine which variable, size or naturalism had the greatest impact on behavior.

The emphasis on naturalistic environments has visitor implications as well. According to some, naturalistic enclosures may encourage visitors to learn more about the natural ecosystems of these species and to develop a deeper respect for the captive animals and their wild counterparts [Coe, 1985; Maple, 1983; Price et al., 1994]. Lukas and Ross' [2014] results from their recent study at the Lincoln Park Zoo supported at least one of these claims. They found that the zoo's newer, more naturalistic great ape exhibit was significantly more effective at improving visitor perceptions toward the animals compared to the traditional, second generation great ape house. However, the results also suggested that the newer exhibit did not significantly increase the visitor's knowledge or awareness of the apes.

Studies in both laboratory and field settings suggest that people prefer the naturalistic environments over barren ones [Moss et al., 2010; Reade and Waran, 1996; Shettel-Neuber, 1988,]. Rhoads and Goldsworthy [1979] showed human subjects pictures of animals in naturalistic zoo settings and pictures of them in more traditional, caged environments and asked them to rank the animals based on multiple facets including dignity and happiness. They found that the public's positive ratings of animals increased as the naturalism of the environment increased. However, other research suggests that the naturalism of the environment only impacts visitors' perception of the enclosure itself, not the animals themselves [Finlay et al., 1984; Finlay et al., 1988; Tofield et al., 2003]. In addition, other studies suggest that visitors spend more time at naturalistic enclosures, specifically when animals are active, and believe the healthy appearance of animals is important. However, these same studies also report that visitors fail to consider other important variables such as the exhibition of stereotypic behaviors, the exhibition of species specific behaviors, or the ability for the animals to get out of visitor view, all of which are extremely important to the well-being of captive animals [Bitgood et al., 1988; Moss et al., 2010; Shettel-Neuber, 1988].

Environmental Enrichment

Along with exhibit progression, the use of environmental enrichment has taken on a pivotal role in modern zoos [Hare et al, 2003; Swaisgood and Shepherdson, 2005]. The need for additional stimuli in captive settings has been documented since 1925 [Yerkes, 1925], yet zoos did not take heed until the late 1970s [Markowitz, 1979; Vivian, 2008]. Today, providing enrichment is considered a standard and essential practice for zoo animal management [Carlstead et al., 1991; Maple and Perkins, 1996; Mason et al., 2007; Shepherdson, 2003]. Environmental enrichment can encompass a range of activities, but all methods have the same overarching purpose: to enhance captive care by providing quality mental and physical stimulation in an otherwise under-stimulating environment [Bloomsmith et al., 1991; Poole, 1998; Shepherdson, 1990; Swaisgood et al., 2001]. Specific goals for enrichment include decreasing inactivity and abnormal behaviors, increasing behavioral diversity specifically through the exhibition of species-specific behaviors, and increasing opportunities for optimal physiological and psychological development [Hare et al., 2003; Nelson and Mandrell, 2005; Young, 2003]. The enrichment used to attain these has traditionally been categorized into five different types: nutritional, occupational, physical, sensory, and social enrichment [Bloomsmith et al, 1991; Laule, 2003].Recently, Hoy et al. [2010] split up the distinctions further into eight discreet categories: auditory, feeding, human/animal interaction, olfactory, social, structural, tactile, and visual enrichment. All of these categories entail the alteration of various environmental components including diet options, social compositions, enclosure size or organization, and the inclusion (or exclusion) of temporary objects.

Environmental enrichment is a significant factor for the welfare improvement of many captive animals [de Azevedo et al., 2007]. It is perhaps most crucial for primates whose heightened cognitive capabilities increase the need for further stimulation [Boere, 2001; Britt, 1998; Honess and Marin, 2006; Murphy, 1976], none more so than the great apes [Maple and Perkins, 1996]. Control, choice and complexity are critical components of the natural primate environments [Badihi, 2006; Humphrey, 1972;

Kulpa-Eddy et al., 2005; Tripp, 1985; Videan et al., 2005]. Living in complex environments gives primates the ability to choose where and how to allocate their time and this choice permits them a certain degree of control [Badihi, 2006]. Because these aspects are reduced in captive settings, enrichment is often provided in an attempt to correct the imbalances [Mench, 1998; Poole, 1990; Sambrook and Buchanan-Smith, 1997]. Introducing novel enrichment or rotating enrichment items increases the unpredictability and thus the complexity of captive enclosures [Line and Morgan, 1991; Pruetz and Bloomsmith, 1992;]. Complexity and control of the environment can be further increased by the complexity or control of the enrichment item itself [Badihi, 2006; Humphrey, 1972; Sambrook and Buchanan-Smith, 1997].

Captive primate environments which fail to provide control, choice, and complexity through the provisioning of enrichment may promote the exhibition of abnormal behavior or stereotypies [Young, 2003]. Stereotypic behaviors are those that are not exhibited in natural, wild conditions [Shepherdson, 1998]. According to Mason et al. [2007], these actions are repetitive and have no apparent function. The two recognized classifications of stereotypies are gross motor actions or whole-body movements (e.g. pacing, rocking, bouncing) and fine motor actions (e.g. hair-pulling, regurgitation, digit-sucking) [Bayne et al., 1993; Mason et al., 2007]. Common stereotypies exhibited by captive primates include regurgitation and reingestion, self-mouthing, ear covering, coprophagy, and rocking [Bayne and Novak, 1998; Marriner and Drickamer, 1994; Novak et al., 2006]. Bollen and Novak [2000] assessed 3,465 primates in zoos to determine how the exhibition of stereotypic behaviors differed among taxonomic groups. They discovered that abnormal behaviors were highest in apes (39.6%), followed by Old Word monkeys (13.8%), and prosimians and New World monkeys were tied for the least (7%). Of the behaviors recorded, fine-motor stereotypies were the most common among all primate groups, followed closely by whole-body stereotypies. Self-injurious behaviors were exhibited the least in primates.

Abnormal rearing and housing conditions were once believed to be the foremost reason for stereotypic behaviors in primates [Harlow and Suomi, 1970; Harlow and Zimmerman, 1959; Mason and Berkson, 1975]. It is true that frequencies of stereotypic behaviors are lower in zoos compared to laboratories [Novak et al., 2006]; however, because most zoo primates are socially grouped and reared, the prevalence of stereotypies in zoos indicates causes that extend past inadequate social environments. Such causes are thought to be an interaction of genetic, maternal, and environmental factors [Novak et al., 2006]. Yet no matter the direct causes, proper environmental enrichment can retard or prevent the development and execution of stereotypic behaviors [Newberry, 1995; Swaisgood et al, 2001]. Swaisgood and Stephenson [2005] conducted a meta-analysis of 25 studies examining the effect of enrichment on the stereotypic behavior of zoo animals, and concluded that the provisioning of enrichment significantly reduced the exhibition of stereotypies 53% of the time.

Environmental enrichment has similar effects on primate stereotypies [Baker, 1999; Barbiers, 1985; Bitnoff, 1996; Bloomstrand et al., 1986; Paquette and Prescott, 1988; Tripp, 1985]. In a group of captive bonobos, enrichment was used to decrease bouts of environmental destruction and infant 'kid-napping' behaviors [Csatádi et al., 2008]. Puzzle feeders given to captive apes have been known to decrease coprophagia, urophagia and other atypical behaviors [Bloomstrand et al., 1986; Brent and Eichberg, 1991; Maki et al., 1989; Nakamichi, 1999; Seymour and Shepherdson, 1991]. Such behaviors have also been decreased in captive orangutan populations using simple browse [Birke, 2002; Maple, 1980; Tripp, 1985]. Wood [1998] demonstrated that foraging and object-manipulation behaviors increased significantly in captive chimpanzees (*Pan troglodytes*) when novel enrichment was provided, while grooming and play behavior increased with previously used enrichment. The use of technology as enrichment has also become a popular avenue to reduce stereotypic behavior in captive apes [Bloomsmith et al., 2000; Boostrom, 2013; Perdue et al., 2012; Wirman, 2013], though this can also increase intragroup aggression [Tarou et al., 2004].

Enrichment is also important for increasing the overall activity levels of primates [Gilloux et al., 1992; Little and Sommer, 2002; Wilson, 1972; Wright, 1995]. Orangutans in particular are subject to increased levels of inactivity and lethargy in captive settings, but such idleness can be decreased with the provisioning of proper enrichment [Barbiers, 1985; Birke, 2002; Pizzutto et al., 2008; Stevenson, 1983; Tarou et al., 2004]. Wright [1995] determined that providing novel enrichment items to the orangutans at the Cheyenne Mountain Zoo significantly decreased the amount of time they spent inactive. Moreover, having novel items increased the amount of time the orangutans manipulated the objects compared to familiar items. At the Topeka Zoo, Tripp [1985] demonstrated that orangutan locomotion and overall activity levels increased in accordance with the amount of enrichment items provided. His study consisted of three environments: the barren enclosure, the exhibit with manipulable items, and the enclosure with edible and manipulable enrichment. The orangutans were most idle in the empty exhibit and least idle in the enclosure with edible and manipulable items. Multi-institutional studies conducted by Wilson [1982] and Perkins [1992] revealed that the provisioning of movable items was one of the most important factors for promoting increased levels of activity in captive orangutans, along with social partners and enclosure size.

Enrichment Policy

The Animal Welfare Act requires enrichment for nonhuman primates in all captive settings [Kulpa-Eddy et al., 2005]. Furthermore, the USDA/APHIS report [1991] lists the provision of manipulable items as one of the five major elements required for proper captive primate environments, along with social grouping, substrate, and foraging opportunities. Though such legal consideration does not apply to other species, it has become an unwritten rule for zoos to provide enrichment programs for all of the animals in their captive care [Reade and Waran, 1996; Swaisgood et al., 2000; Swaisgood and Shepherdson, 2005]. Even more, the accreditation standards guidebook for the Association of Zoos and

Aquariums [2013] states that accredited zoos must implement and follow enrichment policies that promote species appropriate behavior.

Trying to retain a naturalistic exhibit while still providing enrichment items has led many zoos to implement all-natural enrichment policies [Hare et al., 2003; Kutska, 2009]. This usually means that only items with a natural appearance are used as enrichment when the animal is in the public's view; therefore, enrichment items that would be considered non-natural, e.g. plastic boomer balls, barrels, blankets, paper items, are kept from the animal until they reside in holding [Hare et al., 2003]. However, such manmade items have been shown to alleviate psychological stress and encourage species-specific behavior in captive primates [Bayne et al., 1993; Brent et al., 1989; Brent and Belik, 1997; Pruetz and Bloomsmith, 1992; Shepherdson, 1998].

Anderson and Stoppa [1991] used sticks and tennis balls to demonstrate the effectiveness of enrichment at deterring self-aggression in a group of four adult female stump-tailed macaques *(Macaca arctoides)*. They concluded that even though the use of either item decreased the frequency of self-aggression bouts, the tennis balls were better at suppressing the behavior compared to the sticks. Sambrook and Buchanan-Smith [1996] determined an inverse relationship between the amount of controllability of most enrichment items and their perceived naturalism. According to the researchers, those items that promote higher levels of control within the environments, and therefore better for welfare of the animals, (e.g. malleable items, levers, electronic, digital mechanisms) are considered unnatural and therefore deemed undesirable in some zoos.

It is understood that such enrichment policies are based solely on the assumption that the use of non-natural items in a naturalistic enclosure would be aesthetically unpleasant and would thus be frowned upon by visitors [Hare et al., 2003; Kreger et al., 1998; Shepherdson, 1998]. However, some researchers believe that such practices could actually be detrimental to the welfare of the animals [Kutska, 2009; McPhee et al., 1998].

Visitor Perception

The perceptions by visitors of enclosures and programs have become increasingly important to the zoo industry [McPhee et al., 1998; Shepherdson, 1998]. As previously stated, visitors seem to prefer naturalistic enclosures over barren ones. For this reason, non-naturalistic items are generally argued to be distracting and unattractive to the public by some zoo staff [Kreger et al., 1998]. However, the results of several studies suggest otherwise [Kutska, 2009; McPhee et al., 1998; Reade and Waran, 1996; Wood, 1998].

Using multiple types of enclosures, including a barren outdoor grotto housing a polar bear (*Ursus arctos maritimus*), a vegetated outdoor grotto housing a tiger (*Pantera tigris*), a traditional bared outdoor cage housing a lynx (*Lynx canadensis*), and indoor naturalistic exhibit housing a fishing cat (*Prionailurus viverrina*), McPhee et al. [1998] found that enrichment type, natural or non-natural, had little to no effect on visitor perception of the enclosure or the animal. In fact, the outdoor grotto received a higher naturalism rating when non-natural enrichment was used. Kutska's study [2009] on a naturalistic polar bear exhibit at the Central Park Zoo showed similar results. She determined that the naturalism of enrichment items had no effect on the visitor perception of polar bears in general, the zoo, the naturalism of the enclosure, or the specific polar bears housed at the zoo. Instead, the results suggest that the age of the visitor and whether or not they are pet owners have more of an impact on their perception. Perdue et al. [2012] analyzed visitor attitudes of touchscreen technology, an obvious non-natural enrichment, within a captive orangutan enclosure. She found that visitors appreciated the use of technology as enrichment and recognized its benefit for the orangutans. Visitors gave positive remarks on the effect of the enrichment on both the orangutans and themselves.

Research demonstrates that visitor interest in zoo enclosures increases when enrichment items are present, no matter the type of enrichment [Price et al., 1994]. This is especially the case in instances where the animals are using the enrichment [McPhee et al., 1998; Price et al., 1994; Wood, 1998].

Visitors seem to be more concerned with the fact that the animals are given enrichment in general and less concerned with what the items look like [Tofield et al., 2003; Wood, 1998]. For this reason, zoo management should begin basing their enrichment decisions more on the needs of the animal rather than the perceived interests of the visitors [McPhee, 1998; Poole, 1998; Rosenblum and Andrews, 1995].

Enrichment Characteristics

Animal behavior studies have shown that some enrichment objects can be more attractive to animals than others [Sackett, 1966; Humphry 1972, Delfour and Beyer, 2011]. In a study examining the enrichment characteristics that best stimulate the exploratory behavior of pigs, Van de Weerd et al. [2003] determined that the preferential quality of certain properties may change over time. For instance, they found chewable, moveable, and odorous items to be most attractive on day one of provisioning, while edible and destructible items held the pigs' interest more by day five. Overall, it seems the pigs were most occupied by those objects that encouraged foraging behaviors. Such results imply that enrichment efficiency is associated with the exhibition of behaviors that are meaningful or normal to the animal [Schapiro and Bloomsmith, 1995; Swaisgood et al., 2005].

In their study on captive giant pandas (*Ailuropoda melanoleuca*), Swaisgood et al. [2005] used multiple physical properties to analyze the efficiency of enrichment items. Their defined properties included chemo-stimulatory, destructibility, malleability, manipulability, movability, propellability, and tactile stimulatory. Although they found the characteristics did not play a major role in the effectiveness or preferential quality of the enrichment, they did determine that each item promoted different behaviors that could have been associated with their properties (the ball increased play behaviors, branches increased exploratory behaviors, etc.). Because different objects led to different behavioral outcomes, the researchers ascertained that enrichment properties should be taken into consideration when provisioning items.

Differing enrichment characteristics have been shown to have great effect on captive primates. A common find is the preference of destructible items in captive chimpanzees [Brent and Stone, 1998; Pruetz and Bloomsmith, 1992; Shefferly et al., 1993; Videan et al., 2005]. Other examples of primate tactile preferences of enrichment items include the partiality to flexible and circular items in long-tail macaques (*Macaca fascicularis*) [Weld and Erwin, 1990], the bias for moving stimuli over inanimate objects in greater galagos (*Galago crassicaudatus*) and slow lorises (*Nycticebus coucang*) [Jaenicke and Ehrlich, 1972], and the proclivity for moveable objects in bushbabies (*Otolemur garnetti)* [Renner et al., 1992]. Further, Wells et al. [2008] determined that color can also impact the preferential quality of enrichment. Specifically, they found that both chimpanzees and gorillas (*Gorilla gorilla gorilla*) spent significantly more time manipulating red and green items over red ones. Aside from these more discrete and observable physical characteristics, novelty [Brent et al., 1989; Cardinal and Kent, 1998; Line et al., 1989; Menzel, 1971; Paquette and Prescott, 1988], complexity [Butler, 1954; Humphrey, 1972; Sackett, 1966; Sambrook and Buchanan-Smith, 1997], and controllability [Mench, 1998; Vick et al., 2000; Videan et al., 2005] have also been shown to be important properties of primate enrichment.

The individual differences between primate group members' preference for enrichment has also been well documented [Crocket et al., 1989; Hienz et al., 1998; Perkins et al., 1992; Vivian, 2008]. Differences in age [Bloomsmith et al., 1990; Videan et al., 2005], environment [Bloomsmith et al., 1990; Shepherdson et al., 2004], and sex [Pruetz and Bloomsmith, 1992; Novak et al., 1993] can impact which items primates prefer to manipulate or how much time they spend manipulating these items. Thus, institutions should continually assess the effectiveness of their enrichment programs and make appropriate adjustments on a case-by-case basis [Chamove & Anderson, 1989; Swaisgood and Shepherdson, 2005].

Literature Cited

Ancrenaz M et al. 2008. *Pongo pygmaeus*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 10 May 2015.

Anderson JR, Stoppa F. 1991. Incorporating objects into sequences of aggression and self-aggression by Macaca arctoides: An unusual form of tool use. Lab Primate Newslett, 30(1).

Association of Zoos and Aquariums. 2013. Accreditation Standards and Related Policies (2013 edition): 9-10.

Badihi I. 2006. The effects of complexity, choice and control on the behaviour and the welfare of captive common marmosets (*Callithrix jacchus*). [dissertation]. Department of Psychology University of Stirling.

Baker KC. 1999. Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. Zoo Biol 16: 225-236.

Barbiers RB. 1985. Orangutans: Color preference for food items. Zoo Biol 4: 287-290.

Bastian ML, Zweifel N, Vogel ER, Wich SA, van Schaik, CP. 2010. Diet traditions in wild orangutans. Am J Phys Anthro 143: 175-187.

Bayne KAL, Dexter SL, Hurst JK, Strange GM, Hill EE. 1993. Kong™ toys for laboratory primates: Are they really an enrichment or just fomites? Lab Anim Sci 43: 78-85.

Bayne K, Novak M. 1998. Behavioural disorders. In: Bennett B, Abee C, Henrickson R, editors. Nonhuman primates in biomedical research: Diseases. New York: Academic Press. p. 485–500.

Bean A. 1998. The ecology of sex differences in great ape foraging behaviour and hunter gatherer subsistence behavior. [dissertation]. Cambridge: University of Cambridge.

Birke L. 2002. Effects of browse, human visitors and noise on the behavior of captive orangutans. Anim Welf 11: 189-202.

Bitgood S, Patterson D, Benefield A. 1988. Exhibit design and visitor behavior. Environ Behav 20: 474–491.

Bitnoff JA. 1996. The effect of physical environment on the behavior of captive chimpanzees: A comparison of three northern California zoos. [thesis]. California: San Jose State University.

Bloomsmith MA, Brent LY, Schapiro SJ. 1991. Guidelines for developing and managing an environmental enrichment program for nonhuman primates. Lab Anim Sci 41: 372–377.

Bloomsmith MA, Finlay TW, Merhalski JJ, Maple TL. 1990. Rigid plastic balls as enrichment devices for captive chimpanzees. Lab Anim Sci 40*:* 319-322.

Bloomsmith MA, Keeling ME, Lambeth SL. 1990. Videotapes: Environmental enrichment for singly housed chimpanzees. Lab Anim Sci 19: 42-46.

Bloomsmith MA, Ross SK, Baker KC. 2000. Control over computer-assisted enrichment for socially housed chimpanzees. Am J Primatol, 51: 45.

Bloomstrand MA, Riddle K, Alford P, Maple T. 1986. Objective evaluation of a behavioral enrichment device for captive chimps. Zoo Biol 5: 293-300.

Boere V. 2001. Environmental enrichment for Neotropical primates in captivity. Cienc Rural 31: 543-551.

Bollen KS, Novak MA. 2000. A survey of abnormal behavior in captive zoo primates. American Journal of Primatology 51: 47.

Boostrom H. 2013. Problem-solving with orangutans (*Pongo pygmaeus and Pongo abelii*) and chimpanzees (*Pan troglodytes*): Using the IPAD to provide novel enrichment opportunities. [thesis] Texas: Texas A&M University.

Brent L, Lee DR, Eichberg JW. 1989. Evaluation of two environmental enrichment devices for singly-caged chimpanzees (*Pan troglodytes*). Am J Primatol Supplement 1: 65-70.

Brent L, Eichberg JW. 1991. Primate puzzle board: A simple environmental enrichment device for captive chimpanzees. Zoo Biol 10: 353-360.

Brent L, Belik M. 1997. The response of group-housed baboons to three enrichment toys. Lab Anim 31: 81-85.

Brent L, Stone AM. 1998 Destructible toys as enrichment for captive chimpanzees. J Appl Anim Welf Sci 1: 5-14.

Britt A. 1998. Environmental enrichment for apes: A literature review. Field D A. Guidelines for Environ-mental Enrichment. Lon-don: Association of British Wild Animal Keepers, 233-247.

Butler RA. 1954. Incentive condition which influence visual exploration. J Exp Psychol 48: 19-23.

Campbell S. 1984. A new zoo? Zoonooz 55: 4-7.

Cardinal BR, Kent SJ. 1998. Behavioral effects of simple manipulable environmental enrichment on pair-housed juvenile macaques (*Macaca nemestrina*). Lab Primate Newslett 37: 1-5.

Carlstead K, Seidensticker J, Baldwin R. 1991. Environmental enrichment for zoo bears. Zoo Biol 10: 3-16.

Chamove AS, Anderson JR. 1989. Examining environmental enrichment. In: Segal EF, editor. Housing, care and psychological well-being of captive and laboratory primates. New Jersey: Noyes Publications. p 183–199.

Chang TR, Forthman DL, Maple TL. 1999. Comparison of confined mandrill (*Mandrillus sphinx*) behavior in traditional and “ecologically representative” exhibits. Zoo Biol 18: 163-176.

Clarke A, Juno C, Maple T. 1982. Behavioral effects of a change in the physical environment: A pilot study of captive chimpanzees. Zoo Biol 1: 371–380.

Cocks LR. 1998. Investigation of the factors affecting the well-being and survival of orangutans (*Pongo pygmaeus*) in captivity. [thesis]. Western Australia: Curtin University.

Cocks L. 2007. Factors influencing the well-being and longevity of captive female orangutans. Int J Primatol 28: 429-440.

Coe JC. 1985. Design and perception: making the zoo experience real. Zoo Biol 4: 197-208.

Coe JC, Maple T. 1984. Approaching Eden: A behavioral basis for great ape exhibits. AAZPA , 1984 Annual Conference Proceedings, American Association of Zoological Parks and Aquariums, Wheeling, WV, 117-128.

Courtenay J, Groves C, Andrews P. 1988. Inter- or intra-island variation? An assessment of the differences between Bornean and Sumatran orang-utans. In: Schwartz JH, editor. Orang-utan biology. p 19-29.

Crockett CM, Bielitzki J, Carey A, Velez A. 1989. Kong toys as enrichment devices for singly-caged macaques. Lab Primate Newslett 28*:* 21–22.

Csatádi K, Leus K, Pereboom JJM. 2008. A brief note on the effects of novel enrichment on an unwanted behaviour of captive bonobos. Appl Anim Behav Sci 112: 201–204.

de Azevedo CS, Cipreste CF, Young RJ. 2007. Environmental enrichment: A GAP analysis. Appl Anim Behav Sci 102: 329-343.

Delfour F, Beyer H. 2011. Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). *Zoo Biol* 31: 137-150.

Delgado RA Jr., van Schaik CP. 2000. The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. Evol Anthro 9: 201-18.

Edwards SD, Snowdon CT. 1980. Social behavior of captive, group-living orangutans. Int J Primatol 1: 39-62.

Finlay T, Woehr D, Maple T. 1984. Evaluation techniques in zoo environments: Visitor attitudes and animal behavior. In: 1984 Southeastern Psychologcial Association Conference. New Orleans, LA.

Finlay T, Lawrence RJ, Maple TL. 1988. People's perceptions of animals: the influence of zoo environment. Environ Behav 20: 508-528.

Fox EA, van Schaik CP, Sitompul A, Wright DN. 2004. Intra-and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: Implications for the invention of tool use. Am J Phys Anthropol 125: 162-174.

Galdikas BMF. 1984. Adult female sociality among wild orangutans at Tanjung Puting Reserve. In: Small MF, editor. Female primates: Studies by women primatologists. New York: Alan R. Liss. p 217-35.

Galdikas BMF. 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. Int J Primatol 9: 1-35.

Gilloux I, Gurnell J, Shepherdson D. 1992. An enrichment device for great apes. Anim Welf 1: 279–289.

Gold KC. 1997: The conservation role of primate exhibits in the zoo. In: Wallis J, editor. Primate conservation: The role of zoological parks. Oregon: American Society of Primatology. p 43-62.

Groves CP. 1999. The taxonomy of orang-utans. Direktoraat Jenderal Perlindungen dan Koservasi Alam, World Wildlife Fund, Indonesia, and Center for Environmental Research and Conservation (CERC), Columbia University, Jakarta, Indonesia, New York, USA.

Groves CP. 2001. Primate Taxonomy. Smithsonian Institution, Washington. p 298–300.

Hare V, Ripsky D, Battershill R, Bacon K, Hawk K, Swaisgood R. 2003. Giant panda enrichment: Meeting everyone's needs. Zoo Biol 22: 401-416.

Harlow HF, Suomi SJ. 1970. Nature of love: Simplified. Am Psychol 25: 161–168.

Harlow HF, Zimmermann RR. 1959. Affectional responses in the infant monkey. Science 130: 421–432.

Hebert PL, Bard K. 2000. Orangutan use of vertical space in an innovative habitat. Zoo Biol 19: 239–251.

Hienz RD, Zarcone TJ, Turkkan JS, Pyle DA, Adams RJ. 1998. Measurement of enrichment device use and preference in singly caged baboons. Lab Primate Newslett 37: 6-10.

Honess PE, Marin CM. 2006. Enrichment and aggression in primates. Neurosci Biobehav Rev 30: 413-436.

Hoy JM, Murray PJ, Tribe A. 2010. Thirty years later: Enrichment practices for captive mammals. Zoo Biol 29: 303–316.

Humphrey NK. 1972 'Interest' and 'pleasure': Two determinants of a monkey's visual preferences. Perception 1: 395-416.

Jaenicke C, Ehrlich A. 1972. Effects of animate vs inanimate stimuli on curiosity behavior in greater galago and slow loris. Primates 23: 95-104.

Kanamori T, Kuze N, Bernard H, Malim TP, Kohshima S. 2010. Feeding ecology of Bornean orangutans (*Pongo pygmaeus morio*) in Danum Valley, Sabah, Malaysia: A 3-year record including two mast fruiting. Am J Primatol 72: 820-840.

Knott CD. 1998a. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19: 1061-1079.

Knott CD. 1998b. Social system dynamics, ranging patterns and male and female strategies in wild Bornean orangutans (*Pongo pygmaeus*). Am J Phys Anthropol Suppl 26: 140.

Kreger MD, Hutchins M, Fascione N. 1998. Context, ethics, and environmental enrichment in zoo and aquariums. In: Sheperdson DJ, Mellen J, Hutchins M, editors. Second nature: Environmental enrichment for captive animals. Washington, DC: Smithsonian Institution Press. p 59-82.

Kulpa-Eddy JA, Taylor S, Adams KM. 2005. USDA perspective on environmental enrichment for animals. ILAR Journal 46: 83–94.

Kutska D. 2009. Variation in visitor perceptions of a polar bear enclosure based on the presence of natural vs un-natural enrichment items. Zoo Biol 28: 292-306.

Kuze N, Malim TP, Kohshima S. 2005. Developmental changes in the facial morphology of the Borneo orangutan (*Pongo pygmaeus*): Possible signals in visual communication. Am J Primatol 65*:* 353-376.

Laule GE. 2003. Positive reinforcement training and environmental enrichment: Enhancing animal well-being. J Am Vet Med Assoc 223: 969-972.

Leighton M. 1993. Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. Int J Primatol 14: 257-313.

Line SW, Morgan KN. 1991. The effects of two novel objects on the behavior of singly caged adult rhesus macaques. Lab Anim Sci 41: 365–369.

Line SW, Morgan KN, Markowitz H, Strong S. 1989. Influence of cage size on heart rate and behavior in rhesus monkeys. Am J Vet Res 50: 1523-1526.

Little KA, Sommer V. 2002. Change of enclosure in langur monkeys: Implications for the evaluation of environmental enrichment. Zoo Biol 21: 549-559.

Loken B, Spehar S, Rayadin Y. 2013. Terrestriality in the Bornean orangutan (*Pongo pygmaeus morio*) and implications for their ecology and conservation. Am J Primatol 75: 1129-1138.

Lukas KE, Ross S. 2014. Naturalistic exhibits may be more effective than traditional exhibits at improving zoo-visitor attitudes toward African Apes. Anthrozoos 27: 435-455.

MacKinnon J. 1971. The orangutan in Sabah today. Oryx 11: 141-191.

MacKinnon J. 1974. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). Anim Behav 22: 3-74.

Maki S, Alford PL, Bloomsmith MA, Franklin J. 1989. Food puzzle device simulating termite fishing for captive chimpanzees (*Pan troglodytes*). Am J Primatol Supplement 1: 71-78.

Maple TL. 1980. Orang-utan Behavior. New York, NY: Van Nostrand Reinhold Co.

Maple TL. 1983. Environmental psychology and great ape reproduction. Int J Study Anim Probl 4: 295-299.

Maple TL, Finlay TW. 1986. Evaluating the environments of captive non-human primates. In: Benirschke K, editor. Primates: The road to self-sustaining populations. New York: Springer–Verlag. p 479–488.

Maple TL, Perkins LA. 1996. Enclosure furnishings and structural environmental enrichment. In: Kleiman DG, editor. Wild mammals in captivity: Principles and techniques. Chicago: University of Chicago Press. p 212-223.

Maple TL, Stine W. 1982. Environmental variables and great ape husbandry. Am J Primatol 3: 67-76.

Markham RJ, Groves CP. 1990. Weights of wild orangutans. Am J Phys Anthro 81: 1–3.

Markowitz H. 1979. Environmental enrichment and behavioral engineering for captive primates. In: Erwin J, Maple TL, Mitchell G, editors. Captivity and behavior: Primates in breeding colonies, laboratories and zoos. New York: Van Nostrand Reinhold. p 231-238.

Marriner LM, Drickamer LC. 1994. Factors influencing stereotyped behavior of primates in a zoo. Zoo Biol 13: 267-275.

Mason WA, Berkson G. 1975. Effects of maternal mobility on the development of rocking and other behaviors in rhesus monkeys: A study with artificial mothers. Dev Psychobol 8: 197-221.

Mason G, Clubb R, Latham N, Vickery S. 2007. Why and how should we use environmental enrichment to tackle stereotypic behavior? Appl Anim Behav Sci 102: 163-188.

Masterson TJ, Leutenegger W. 1992. Ontogenetic patterns of sexual dimorphism in the cranium of Bornean orang-utans (*Pongo pygmaeus pygmaeus*). J Hum Evol 23*:* 3-26.

McPhee M. Foster JS, Sevenich M, Saunders CD. 1998. Public perceptions of behavioral enrichment: Assumptions gone awry. Zoo Biol 17: 525-534.

Mench JA. 1998. Environmental enrichment and the importance of exploratory behavior. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: Environmental enrichment for captive animals. Washington DC: Smothsonian Institute Press. p 30-46.

Menzel EW. 1971. Group behavior in young chimpanzees: Responsiveness to cumulative novel changes in a large outdoor enclosure. J Comp Physiol Psychol 74: 46-51.

Mitani JC. 1989. Orangutan activity budgets: Monthly variations and the effects of body size, parturition, and sociality. Am J Primatol 18: 87-100.

Mitani JC, Grether GF, Rodman PS, Priatna D. 1991. Associations among wild orang-utans: Sociality, passive aggregations or chance? Anim Behav 42: 33-46.

Mitra Setia T, Delgado RA, Utami Atmoko SS, Singleton I, Van Schaik CP. 2009. Social organization and male-female relationships Orangutans, In: Wich SA, Atmoko SSU, Setia TM, van Schaik CP, editors. Orangutans: Geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 245-253.

Moss A, Esson M, Francis D. 2010. Evaluation of a third-generation zoo exhibit in relation to visitor behavior and interpretation use. J Interpret Res 15: 11-28.

Morrogh-Bernard H, Husson S, Page SE, Rieley JO. 2003. Population status of the Bornean orang-utan (*Pongo pygmaeus*) in the Sebangau peat swamp forest, Central Kalimantan, Indonesia. Biol Cons 110: 141-152.

Morrogh-Bernard HC et al. 2009. Orangutan activity budgets and diet. In: Wich SA, Atmoko SSU, Setia TM, van Schaik CP, editors. Orangutans: Geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 119-134.

Muir CC, Galdikas BM, Beckenbach AT. 2000. mtDNA sequence diversity of orangutans from islands of Borneo and Sumatra. J Mol Evol 51: 471–480.

Murphy DE. 1976. Enrichment and occupational devices for orangutans and chimpanzees. International Zoo News 23: 24-26.

Nakamichi M. 1999. Spontaneous use of sticks as tools by captive gorillas (*Gorilla gorilla gorilla*). Primates 40: 487-498.

Nelson RJ, Mandrell TD. 2005. Enrichment and nonhuman primates: “First, do no harm”. ILAR Journal 46: 171-177.

Newberry RC. 1995. Environmental enrichment: Increasing the biological relevance of captive environments. Appl Anim Behav Sci 44: 229-243.

Novak MA, Meyer JS, Lutz C, Tiefenbacher S. 2006. Deprived environments: Developmental insights from primatology. In: Mason GJ, Rushen J, editors. Stereotypic animal behaviour: Fundamentals and applications to welfare. 2nd ed. Wallingford, UK: CABI, 153-189.

Novak MA, Musante A, Munroe H, O'Neill PL, Price C, Suomi SJ. 1993. Old, socially housed rhesus monkeys manipulate objects. Zoo Biol 12: 285-298.

Ogden JJ, Finlay TW, Maple TL. 1990. Gorilla adaptations to naturalistic environments. Zoo Biol 9: 107-121.

O'Neill PL, Novak MA, Suomi SJ. 1991. Normalizing laboratory-reared rhesus macaque *(Macaca mulatta*) behavior with exposure to complex outdoor enclosures. Zoo Biol 10: 237-245.

Paquette D, Prescott J. 1988. Use of novel objects to enhance environments of captive chimpanzees. Zoo Biol 7: 15–23.

Perdue BM, Clay AW, Gaalema DE, Maple TL, Stoinski TS. 2012. Technology at the zoo: The influence of a touchscreen computer on Orangutans and zoo visitors. Zoo Biol 31: 27-39.

Perkins L. 1992. Variables that influence the activity of captive orangutans. Zoo Biol 1: 177-186.

Perkins SE, Burnett DE, Rice TR, Staley C, Weick BG. 1992. Evaluation of the use of novel objects by adult male *Macaca mullatta*, singly housed in Horsfal isolators. Lab Primate Newslett 31: 34-36.

Pizzutto CS, Dias MN, Geronymo MGFB, Correa SRH, Viau P, Beresca AM. 2008. Effect of environmental enrichment on behavioral and endocrine aspects of a captive orangutan (*Pongo pygmaeus*). Lab Primate Newslett 47: 10-14.

Poole TB. 1990. Environmental enrichment for marmosets. Anim Technol 41: 81-86.

Poole TB. 1987. Social behavior of a group of orangutans (*Pongo pygmaeus*) on an artificial island in Singapore Zoological Gardens. Zoo Biol 6: 315-330.

Poole TB. 1998. Meeting a mammal's psychological needs: Basic principles. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: Environmental enrichment for captive animals. Washington DC: Smithsonian Institution Press. p 83-94.

Price E, Ashmore L, McGiven A. 1994. Reactions of zoo visitors to free-ranging monkeys. Zoo Biol 13: 109-118.

Pruetz JD, Bloomsmith MA. 1992. Comparing two manipulable objects as enrichment for captive chimpanzees. Anim Welf 1: 127-137.

Reade LS, Waran NK, 1996. The modern zoo: How do people perceive zoo animals? Appl Anim Behav Sci 47: 109-118.

Renner MJ, Bennett AJ, Ford ML, Pierre PJ. 1992. Investigation of inanimate objects by the greater bushbaby (*Otolemur garnetti*). Primates 33*:* 315–328.

Rhoads DL, Goldsworthy RJ. 1979. The effects of zoo environments on public attitudes toward endangered wildlife. Int J Environ Stud 13: 283-287.

Rijksen HD, Meijaard E. 1999. Our vanishing relative: The status of wild orang-utans at the close of the 20th century. Dordrecht (Netherlands): Kluwer Academic Publishers. p 480.

Rodman PS. 1979. Individual activity patterns and the solitary nature of orangutans. In: Hamburg DA, McCown ER, editors. The great apes. San Francisco: Benjamin/Cummings Pub. p 234-255.

Rodman PS. 1984. Foraging and social systems of orangutans and chimpanzees. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates. New York: Columbia University Press. p 134-160.

Rodman PS. 1988. Diversity and consistency in ecology and behavior. In: Schwartz JH, editor. Orang-utan biology. New York: Oxford University Press. p 31-50.

Rosenblum LA, Andrews MW. 1995. Environmental enrichment and psychological well-being of nonhuman primates. In: Abee CR, Mansfield K, Tardif SD, Morris T, editors. Nonhuman primates in biomedical research: Biology and management. New York: Academic Press. p 101-112.

Rowe N. 1996. The pictorial guide to the living primates. East Hampton (NY): Pogonias Press. p 263.

Sackett GP. 1966. Development of preference for differentially complex patterns by infant monkeys. Psychon Sci 6: 441-442.

Sambrook TD, Buchanan-Smith HM. 1996. What makes novel objects enriching? A comparison of the qualities of control and complexity. Lab Primate Newslett 35: 1-4.

Sambrook TD, Buchanan-Smith HM. 1997. Control and complexity in novel object enrichment. Anim Welf 6: 207-216.

Schapiro SJ, Bloomsmith MA. 1995. Behavioral effects of enrichment on singly-housed yearling rhesus monkeys: An analysis including three enrichment conditions and a control group. Am J Primatol 35: 89–101.

Seymour S, Shepherdson D. 1991. A puzzle feeder for orangutans. Animal Keepers' Forum 18: 230-232.

Shepherdson DJ. 1990. Environmental enrichment: Back to the future. In: 1990 15th Annual Symposium of the Association of British Wild Animal Keepers. Atherstone, Warwickshire. p 42-52.

Shepherdson DJ, 1998. Introduction: Tracing the path of environmental enrichment in zoos. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: Environmental enrichment for captive animals. Washington: Smithsonian Institution Press. p 1–12.

Sheperdson DJ. 2003. Environmental enrichment: Past, present and future. Int Zoo Yearb 38: 118-124.

Shepherdson DJ, Carlstead KC, Wielebnowski N. 2004. Cross-institutional assessment of stress responses in zoo animals using longitudinal monitoring of fecal corticoids and behaviour. Animal Welf 13: 105-113.

Shefferly N, Fritz J, Howell S. 1993. Toys as environmental enrichment for captive juvenile chimpanzees (*Pan troglodytes*). Lab Primate Newslett 32: 7-9.

Shettel-Neuber J. 1988. Second and third generation zoo exhibits: A comparison of visitor, staff, and animal responses. Environ Behav 20: 452-473.

Singleton I, Wich S, Husson S et al. 2004. Orangutan population and habitat viability assessment: Final report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Singleton I, Wich SA, Griffiths M. 2008. *Pongo abelii*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 10 May 2015.

Sodaro C. 2007. Orangutan species survival plan husbandry manual. Chicago: Chicago Zoological Society.

Stevenson MF. 1983 The captive environment: Its effect on exploratory and related behavioural responses in wild animals. In: Archer J, Birke L, editors. Exploration in animals and humans. Wokingham, UK: Van Nostrand Rheinhold. p 176-197.

Swaisgood RR, Lindburg DG, Zhou X, Owen MA. 2000. The effects of sex, reproductive condition and context on discrimination of conspecific odours by giant pandas. Anim Behav 60: 227–37.

Swaisgood RR, Sheperdson DJ. 2005. Scientific approaches to enrichment and stereotypies in zoo animals: What's been done and where should we go next? Zoo Biol 24: 499-518.

Swaisgood RR, White AM, Zhou X, Zhang G, Lindburg DG. 2005. How do giant pandas (*Ailuropoda melanoleuca*) respond to varying properties of enrichments? A comparison of behavioral profiles among five enrichment items. J Comp Psychol 119: 325-334.

Swaisgood RR, White AM, Zhou X, Zhang H, Zhang G, Wei R, Hare V, Tepper EM, Lindburg DG. 2001. A quantitative assessment of the efficacy of an environmental enrichment programme for giant pandas. Anim Behav 61: 447-457.

Tarou LR, Kuhar CW, Adcock D, Bloomsmith MA, Maple TL. 2004. Computer-assisted enrichment for zoo-housed orangutans (*Pongo pygmaeus*). Anim Welf 13: 445-453.

Taylor AB, van Schaik CP. 2007. Variation in brain size and ecology in Pongo. J Hum Evol *52:* 59-71.

te Boekhorst IJA, Schürmann CL, Sugardjito J. 1990. Residential status and seasonal movements of wild orang-utans in the Gunung Leuser Reserve (Sumatera, Indonesia). Anim Behav 39: 1098-1109.

Tobach E, Greenberg G, Radell P, McCarthy T. 1989. Social behavior in a group of orang-utans (*Pongo pygmaeus abelii*) in a zoo setting. Appl Anim Behav Sci 23: 141-154.

Tofield S, Coll R, Vyle B, Bolstad R. 2003. Zoos as a source of free choice learning. Res Sci Technol Educ 21: 67–99.

Tripp JK. 1985. Increasing activity in captive orangutans: Provision of manipulable and edible materials. Zoo Biol 4: 225-234.

USDA-APHIS [US Department of Agriculture-Animal and Plant Health Service].1991. 9 CFR Part 3: Animal Welfare Standards; Final Rule. Federal Register56(32):6426–6505.

Utami S, Wich SA, Sterk EHM, van Hoof JARAM 1997. Food competition between wild orangutans in large fig trees. Int J Primatol 18: 909-927.

Van de Weerd HA, Docking CM, Day JEL, Avery PJ, Edwards SA. 2003. A systematic approach towards developing environmental enrichment for pigs. Appl Anim Behav Sci 84: 101–118.

van Schaik CP. 1999. The socioecology of fission-fusion sociality in orangutans. Primates 40: 69-86.

van Schaik CP, Marshall AJ, Wich SA. 2009. Geographic variation in orangutan behavior and biology. In: Wich SA, Atmoko SSU, Setia TM, van Schaik CP, editors. Orangutans: Geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 351-361.

van Schaik CP, Monk KA, Robertson JM. 2001. Dramatic decline in orang-utan numbers in the Leuser Ecosystem, Northern Sumatra. Oryx 35: 14-25.

van Schaik CP, Preuschoft S, Watts DP. 2004. Great ape social systems. In: Russon AE, Begun DR, editors. The evolution of thought: evolutionary origins of great ape intelligence. Cambridge (England): Cambridge Univ Press. p 190-209.

van Schaik CP, van Hooff JARAM. 1996. Toward an understanding of the orangutan's social system. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge (England): Cambridge Univ Press. p 3-15.

Vick SJ, Anderson JR, Young RJ. 2000. Maracas for *macaca*? Evaluation of three potential enrichment objects in two species of zoo-housed macaques. Zoo Biol 19: 181–191.

Videan EN, Fritz J, Schwandt ML, Smith HF, Howell S. 2005. Controllability in environmental enrichment for captive chimpanzees (*Pan troglodytes*). J Appl Anim Welf Sci 8: 117-130.

Vivian M. 2008. Operant methodology out of the lab and applied to enrichment with captive chimpanzees *(Pan troglodytes).* [dissertation]. Hamilton, New Zealand: University of Waikato.

Weld K, Erwin J. 1990. Provision of manipulable objects to cynomolgus macaques promotes species-typical behavior. Am J Primatol 20: 243 (Abstract).

Wells DL, McDonald CL, Ringland JE. 2008. Color preferences in gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). J Comp Psychol 122: 213.

Wich SA, et al. 2008. Distribution and conservation status of the orang-utan (Pongo spp.) on Borneo and Sumatra: How many remain? Oryx 42: 329-339.

Wich SA, et al. 2012. Understanding the impacts of land-use policies on a threatened species: Is there a future for the Bornean orang-utan?. *PLoS One 7*: e49142.

Wich SA, Utami-Atmoko SS, Setia TM, Djoyosudharmo S, Geurts ML. 2006. Dietary and energetic responses of Pongo abelii to fruit availability fluctuations. *Int J Primatol 27*: 1535-1550.

Williamson DK, Dunbar RM. 1999. Energetics, time budgets and group size. In: Lee PC, editor. Comparative primate socioecology, Cambridge: Cambridge University Press. p 320–338.

Wilson CC. 1972. Spatial factors and the behavior of nonhuman primates. Folia Primatol 18: 256-275.

Wilson S. 1982. Environmental influences on the activity of captive apes. Zoo Biol 1: 201-209.

Winkler LA. 1989. Morphology and relationships of the orangutan fatty cheek pads. Am J Primatol 17: 305-319.

Wirman H. Orangutan play on and beyond a touchscreen. In: Cleland, K., Fisher, L. & Harley, R., editors. 2013 Proceedings of the 19th International Symposium of Electronic Art. Sydney: Australia.

Wood W. 1998. Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes*). Zoo Biol 17: 211-230.

Wright BW. 1995. Novel item enrichment program reduces lethargy in orangutans. Folia Primatol 65: 214-218.

Yeager C. 1999. Orangutan Action Plan. Report for Direktorat Jenderal Perlindungan dan Konservasi Alam, World Wildlife Fund for Nature Indonesia, and CERC. Jakarta, Indonesia. p 30.

Yerkes, R. M. 1925. Almost human. Cape J. New York: The Century Company.

Young RJ. 2003. Environmental enrichment for captive animals. Oxford, UK: Blackwell Science.

Zhang Y, Ryder OA, Zhang Y. 2001. Genetic divergence of orang-utan subspecies (*Pongo pygmaeus*). J Mol Evol 52: 516–526.

Zucker EL, Dennon MB, Puleo SG, Maple TL. 1986. Play profiles of captive adult orangutans: A developmental perspective. Dev psychobiol 19: 315-326.

CHAPTER 2:

EFFECTS OF NATURAL VS NON-NATURAL ENRICHMENT ITEMS ON CAPTIVE ORANGUTAN BEHAVIOR

Crosby, Kaylin S. and Dodson, Gary

Prepared for Zoo Biology

Abstract

Naturalistic enclosures are known to reduce stereotypic actions in captive animals, as well as increase the exhibition of natural behaviors. Such exhibits also promote longer visitor stay time, thereby encouraging higher visitor education and awareness. However, the perceived naturalism of provisioned enrichment items within these enclosures seems to have little impact on overall visitor perceptions. Even so, some zoos are forbidding the use of non-natural enrichment items on exhibit. Until now, there has been no testing of the potential effect that these two categories of enrichment items might have on the behavior of the animals being exhibited. This study aimed to examine the impact on orangutan behaviors, social interactions, and space use when they are exposed to non-natural versus natural enrichment items. Using the orangutan populations from the Fort Wayne Children's Zoo and the Louisville Zoo, I tested the hypothesis that naturalistic enrichment items promote desired behaviors (e.g. brachiating, increased activity) or at least suppress undesired behaviors (e.g. stereotypies, excessive aggression, destruction) at the same rate as non-natural items. Given that particular objects may have disproportionate effects on behavior outside of their categorization as natural or non-natural, the enrichment items were also analyzed based on their specific characteristics, such as texture, destructibility, or size. The results suggested that the naturalism of the enrichment items does not significantly impact the overall behavior composite of captive orangutans. Even so, such categories may impact behaviors on an individual basis, especially social behaviors. Further analyses revealed that physical properties of enrichment, whether categorized as natural or not, had predictive effects on solitary and social behaviors. For this reason, enrichment policies should place emphasis on specific item characteristics instead of their perceived naturalism. Ultimately, the results provide zoos with additional advice for developing optimal orangutan enrichment policies.

Introduction

Zoo exhibits have gone through major transformations over the past 50 years, culminating in the current focus on the importance of naturalistic enclosures [Coe and Maple, 1984; Moss et al., 2010; Shettel-Neuber, 1998]. This emphasis has arisen not only in an effort to increase visitor learning opportunities about the natural ecosystems of the housed species, but also to improve zoo animal welfare [Gold, 1997; Lukas and Ross, 2014; Moss et al., 2010; Price et al., 1994]. Naturalistic enclosures have been shown to increase visitor stay time as well as encourage a deeper appreciation for the captive animals and their wild counterparts [Coe, 1985; Lukas and Ross; 2014; Price et al., 1994; Maple, 1983]. Compared to the more barren traditional zoo enclosures, naturalistic environments provide captive animals with more opportunities to express species-specific behaviors [Campbell, 1984; Newberry, 1995], and in doing so, can also decrease the rate of abnormal behaviors, also known as stereotypies [Maple and Stine, 1982; O'Neill et al., 1991].

Along with exhibit progression, the use of environmental enrichment has taken on a pivotal role in modern zoos [Hare et al., 2003; Swaisgood and Shepherdson, 2005]. Environmental enrichment, the practice of providing quality mental and physical stimulation in an otherwise under stimulating environment [Mason et al., 2007; Swaisgood et al., 2000], is considered essential for zoo animal welfare [Carlstead et al., 1991; Maple and Perkins, 1996; Newberry, 1995; Shepherdson, 2003; Young, 2008]. The zoo community recognizes several types of environmental enrichment, including social enrichment, occupational enrichment, and physical enrichment [Bloomsmith et al., 1991]. The most common form of enrichment, and the one on which this study focuses, is the provisioning of temporary items for manipulation or other interaction by the animals [Mason et al., 2007; Swaisgood et al., 2005]. As some zoos have implemented policies requiring all public exhibit components to have a natural appearance [Hare et al., 2003; Kutska, 2009], the challenge of providing sufficient naturalistic items for animal enrichment has been revealed [McPhee et al., 1998].

The case for all-natural exhibits has been advocated in part based on the claim that non-naturalistic enrichment items are distracting and unappealing to the public, especially when used within a more naturalistic enclosure [Kreger et al., 1998]. However, the results of several studies would suggest otherwise [Kutska, 2009; McPhee et al., 1998; Reade and Waran, 1996]. Even though visitors appear to prefer naturalistic enclosures over traditional ones [Lukas and Ross, 2014, Moss et al., 2010; Price et al., 1994], the naturalistic properties of the enrichment items used within the exhibit do not seem to impact the visitor's perception of the space [Kutska, 2009; McPhee et al., 1998]. Therefore, some of the decisions on enrichment may be based solely on a zoo's philosophy regarding exhibit appearance [McPhee et al., 1998].

Enrichment is perhaps most crucial for primates whose heightened cognitive capabilities increase the need for further stimulation [Boere, 2001; Honess and Marin, 2006], none more so than the great apes [Maple and Perkins, 1996]. Along with a decrease in overall activity levels, apes tend to express higher levels of abnormal or unwanted behaviors when enrichment is not provided [Baker, 1999; Barbiers, 1985; Bloomstrand et al., 1986; Tripp, 1985; Wright, 1995]. Orangutans in particular are subject to increased levels of inactivity and lethargy in captive settings [Barbiers, 1985; Birke, 2002]. However, such indolence can be decreased with the provisioning of manipulable enrichment [Perkins, 1992; Tripp, 1985; Wilson, 1982; Wright, 1995].

This study attempted to reveal the extent to which positively connoted captive orangutan behaviors are expressed in the context of a purely naturalistic exhibit. Using the captive orangutan populations at the Fort Wayne Children's Zoo and the Louisville Zoo, I tested the effect that the exclusion of all non-natural items from exhibit areas has on ape behavior. Because physical properties of enrichment items can impact animal behavior [Badihi, 2006; Swaisgood et al., 2005], the items were also examined based on their specific characteristics, such as texture, destructibility, or size.

Methods

Subjects

The study population consisted of seven captive orangutans: three at the Fort Wayne Children's Zoo in Indiana and four at the Louisville Zoo in Kentucky (Table 1). The sample was composed of three flanged males and four adult females, ranging from 20 to 31 years of age. Throughout the study, the subjects were exhibited in groups of one to three. At the Fort Wayne Children's Zoo, the male was always on exhibit with one or both of the females. The Louisville Zoo employed a random rotational exhibit system and the orangutan group composition varied from day to day. The possible groupings included solitary animals, both females, one female with one male, or both females with one male. The two males were never housed together.

Enclosures

The exhibit areas where observations occurred in the two zoos were indoor enclosures. Both areas provided public viewing via paneled glass windows on the front walls. The two exhibits consisted of multiple vertical levels with permanent climbing structures (see appendix).

Fort Wayne Children's Zoo

This indoor enclosure had a total volume of 1,620 m^3 with a rectangular shape, painted concrete walls, a concrete floor, and a galvanized metal mesh ceiling. Three rows of skylights were built into the ceiling, and the back and middle rows of skylights were visible from the public viewing area. The viewing panels were positioned on the front wall at the mid-level of the enclosure. The left wall of the exhibit had two mesh doors leading to the holding area. The zoo keepers periodically led behavioral training sessions at these doors throughout the day. A smaller mesh window was located at the front end of the left wall. This was where the orangutans were given their daily afternoon meals. The right wall held two glass windows with views to the outdoor langur exhibit. Four large, manufactured trees were positioned

throughout the space to allow for vertical and horizontal arboreal movement in the exhibit. Numerous ropes and fire hoses hung from the ceiling and were intertwined throughout the exhibit. A ground watering system was employed to flood the concrete floor and encourage the orangutans to utilize their vertical space.

Louisville Zoo

The Islands area employed a rotational system for five species through four exhibits. Three of the four were outdoor exhibits, but of these, one was not used by the orangutans for safety reasons. For comparison with the Fort Wayne population, observations were restricted to the single indoor exhibit. This enclosure had a trapezoidal floor shape with a total volume of 555 m^3. The public viewing windows were located on the base of the front wall. The side walls were concrete and the entire back wall was galvanized mesh. The keeper area was located on the other side of this mesh wall. Approximately 12 inches of wood shavings covered the floor, and the ceiling was composed of flexible metal mesh. Clear panels above the flexible mesh allowed sunlight into the enclosure. Two metal platforms and a concrete overhang protruding from the walls created more horizontal space. The exhibit included several permanent features to allow and encourage vertical movement; including two firehose hammocks, several long metal bamboo culms, many intertwined vines, and a large teepee structure made from thick tree trunks.

Holding areas

Observations were also conducted in the holding areas of the Louisville Zoo. All orangutans were kept solitary in holding. The four possible orangutan holding units were similar in size and structure. These enclosures had concrete floors of ca. 3 x 5 m, three concrete walls and one metal mesh wall. There was a small skylight in each of the stalls' ceilings. All of the enclosures included a small metal mesh shelf for additional resting space. Overall, these units were structurally simple, though all of them

had at least one rope for climbing and two of them included larger, permanent hanging structures. New hay was provided each night for nesting substrate. Metal chutes connected all but one of the holding areas, so when possible the orangutans were also given access to one of these chutes while in holding.

Potential Environmental Effects

The main aspects of the orangutans' daily routine, such as diet and training sessions, were kept constant throughout the study. However, research in zoo settings is still subject to the influence of contingencies beyond the investigator's control. The large number of observation days was expected to minimize the possibility of missing any significant data trends; however, uncontrolled variables should still be taken into account and include the following. The flooded floor design at Fort Wayne results in the orangutans spending more time on the tree structures [Hebert and Bard 2000], whereas access to the floor at Louisville may lend itself to more quadrupedal and bipedal walking. The Fort Wayne exhibit also had more locations for the animals to be out of visitors' view. As previously stated, the social composition of Louisville's group could change daily compared with Fort Wayne's static combination. Finally, a pregnancy occurred during data collection at Fort Wayne, and while an impact on social behavior was assumed, it would not be expected to differ between natural and non-natural enrichment days.

Enrichment

Each zoo's enrichment item collection was analyzed and divided into two categories: natural and non-natural. Because the specific enrichment items that fit into each category differed across zoos, the categories differentiating the items were broad by necessity (Table 2). Natural items included those that occur in nature or clearly resemble objects in nature in appearance or composition. Objects that did not meet these criteria were therefore considered non-natural. The specific items at each zoo that qualified for one of the two categories were determined in consultation with zoo staff prior to the start of the

research. To suppress any possible effects due to novelty, neither zoo was asked to include objects that were not already part of their enrichment item repertoire.

The main objective of this study was to determine whether naturalistic enrichment items significantly promote desired behaviors or suppress undesired behaviors at the same rate as non-natural items (Table 3). By using comprehensive behavioral categories as the dependent variable, this question could be addressed regardless of the specific manners that any individual items were used. However, since particular items could have had disproportionate effects on orangutan behavior, the items were also analyzed based on their specific characteristics beyond the distinction of natural/non-natural. For example, it is possible that characteristics of objects such as texture, destructibility, or size could be correlated with the exhibition of certain behavioral outcomes. Rather than trying to anticipate all such characteristics beforehand, this possibility was empirically examined *a posteriori*. All items used within the observation periods were characterized as thoroughly as possible and then grouped by the most definitive properties (Table 4).

Data Collection

Observations were conducted from the public viewing areas at both zoos. Observations took place from July to November 2014. Data collection began as soon as orangutans were let into their daytime enclosures (0900 at Fort Wayne and 1000 at Louisville) and lasted approximately 4 h. Holding observations were conducted at Louisville Zoo directly following the public enclosure observations, from 1400-1630. Observations were spread evenly throughout the days of the week. Seven observers collected data on the subjects: the primary investigator and three assistants for each zoo. The six assistants were trained by the primary investigator and required to surpass a preset inter-observer reliability criterion before beginning data collection. Specifically, each assistant conducted multiple 30 min preliminary sessions alongside, but without input from, the primary investigator. All assistants continued this training process until at least 85% of their observations matched those of the primary

investigator for five consecutive mock sessions. The primary investigator also conducted follow up sessions with each assistant half way through the data collection period to ensure reliability.

A predetermined schedule was used to offer enrichment items from each category between days. The keepers set up the assigned enrichment each morning before moving orangutans into the exhibit. Individual orangutan behavior was observed and recorded using instantaneous scan sampling [Altmann, 1974]. The groups were observed for 30 min sessions and all predefined behaviors (Table 5) for each individual were recorded at 1 min intervals throughout that period. At least five 30 min sessions occurred each observation day. As each behavior was noted, the proximity of the subjects to other individuals (Table 6) was also recorded. During the recordings a modifier (the subject being acted upon or acted with) for each of the behaviors was also identified and recorded when appropriate. The location of each individual within the enclosure was also noted at 5 min intervals. To avoid bias, every scan was performed from left to right of the enclosure. At the onset of each on-exhibit 30 min session, the number of visitors present was recorded as 0 (no visitors), 1 (≤ 15 visitors), 2 (16 – 50 visitors), or 3 (> 50 visitors). Observations were documented in spreadsheet software via a tablet or laptop. To facilitate quick and reliable recording, observers used a shorthand system created by the primary investigator in which each behavior of the ethogram was linked to a computer key character.

The ethogram elements were not mutually exclusive; instead, the recorded behaviors were based on a behavioral hierarchy (Figure 1). If more than one behavior occurred simultaneously, the behavior from the highest tier was recorded. If multiple observed behaviors were from the same tier, the most active behavior was recorded. Emphasis was placed on those behaviors deemed positive for orangutans (e.g., increased activity, arboreal locomotion, foraging, tool use) and on those deemed negative (e.g., exhibit destruction, stereotypies, excessive aggression, self-mutilation).

Data Analysis

Activity Budgets

The complete on-exhibit data set comprised 105.5 h of observations across 42 d for natural enrichment and 108 h across 43 d for non-natural enrichment. There were also 27 d during the study when keepers inadvertently placed items from both categories on exhibit. The data from these 'mixed' days were not used in the comparative analysis but were included in the Canonical Correspondence Analysis (see below). To determine whether the use of natural versus non-natural enrichment items have significantly different impacts on the management of desired and undesired behaviors, raw counts for all predetermined behaviors were calculated for each individual animal under both enrichment categories. These counts were then assembled into broader behavioral categories for analysis (Table 7). Though nesting behavior was an intended behavior of interest, this behavior was never observed during the study and was omitted from the analyses.

The initial analysis was conducted on the compiled activity budgets using a blocked, two-way (orangutan x enrichment category) Multivariate Analysis of Covariance (MANCOVA: Wilks' λ), which controlled for crowd size. The behaviors that were not independent of others (inactive, proximity, head cover, and tool use) were excluded from this compound analysis. Subsequent blocked ANCOVAs were then conducted on the averaged rates of all separate behaviors. The opportunities to display the head covering behavior may have been higher when given non-natural enrichment based merely on the size and structure of those items alone, so a separate analysis was conducted for this behavior in which the opportunity to exhibit this behavior for each day was weighted and used as another covariate. The percentages were transformed using arcsine/square root transformations.

The complete holding area data set consisted of 33 h of observations across 12 d for natural enrichment and 37.5 h of observations across 13 d for non-natural enrichment. Separate, two-way ANOVAS (orangutan x enrichment category) were conducted independent of the exhibit observations.

Because the orangutans were kept solitary in holding, social behaviors were not included in the analyses. However, nesting behavior was observed in holding and therefore investigated. All other behavioral categories were held constant between on and off exhibit analyses.

Space Use

Following the example of White and colleagues' [2003], the enclosures were sectioned for recording purposes. Firstly, both exhibits were divided into two vertical levels: lower and upper. The enclosures were then further divided into three horizontal sections: left, middle, right. Finally, the exhibits were sectioned in half from front to back. The final grid system included 12 sectors. These divisions were based on distinctive structural components of each space. As previously stated, location points were recorded at 5 min intervals over the 30 min sessions, resulting in seven location points per session and per individual animal for each enrichment category. Each orangutan's location points from all sessions were combined and inserted into blocked, two-way (orangutan x enrichment category) MANCOVA (Wilks' λ), controlling for crowd size. The location points were then examined separately for vertical levels (lower and upper) and horizontal planes (front and back). These location points were inserted into separate ANCOVAs, controlling for crowd size, to determine if the enrichment category affected how much time the orangutans spent near the public viewing area and how much time they spent in the lower sector. The percentages were transformed using arcsine/square root transformations. All activity budget and space use analyses were conducted in Minitab as two-tailed tests with a critical level of 0.05.

Enrichment Characteristics

To determine whether enrichment characteristics have predictive effects on behavior outcomes, the recorded enrichment properties and behaviors for each on-exhibit observation day were analyzed using Canonical Correspondence Analysis (CCA) in the vegan package of R 2.14 [R Development Core

Team 2013; Oksanen, 2013]. The CCA model was chosen based on its ability to compare two matrices through a multiple linear regression approach.

Canonical Correspondence Analyses are commonly used in community ecology to assess species distribution in specific environmental sites. For the current study, the enrichment characteristics were the "environmental sites" for the first matrix, while the observed behaviors were the "species" for the second matrix. In this model, biplot scaling was employed and the behaviors were optimized. An ANOVA-like permutation for the CCA was used to assess significance of variable constraints. A separate CCA was conducted for holding observations using the same formatting.

Results

Activity Budgets

The MANCOVA for on-exhibit observations did not indicate a main effect of enrichment category on orangutan behavior ($F_{1,16}$=1.301, p=0.293; Table 8). However, results from separate ANCOVAs revealed that enrichment categories had significant impacts on behaviors on an individual basis (Table 9). Non-natural enrichment was associated with more affiliative social interactions, more time spent in the proximity of conspecifics, and more instances of head covering (Figure 2). Although the amount of time spent manipulating an enrichment item was not impacted by enrichment category (Object manipulation, Table 8), the percentage of time the orangutans held the items in their pocession, with or without obvious manipulation, was significantly greater for non-natural than natural items (Time in possession, Table 9). The separate ANOVA's for the holding observations revealed no significant impact of enrichment category on any behaviors (Table 10 and Table 11).

Space Use

The MANCOVA examining the twelve location vectors indicated that the different enrichment categories did not affect exhibit space use ($F_{1,12}$=1.766, p=0.119;Table 12). Subsequent ANCOVAs

determined a significant effect on only one of the twelve location sectors: the right, lower, back sector (Table 12). After further collapsing the sectors into vertical and horizontal planes and analyzing them individually via separate ANCOVAs, there was no indication that the enrichment categories had any significant effects on the time the orangutans spent in these broad regions of the exhibit space (Figure 3).

Enrichment Characteristics

A significant relationship was found between the on-exhibit behaviors and enrichment characteristics ($F_{1,104}$=6.126, P=0.005). The CCA for the on-exhibit observations resulted in 29.2% of the total variance in the observed behaviors being explained by the enrichment characteristics, with the first three ordination axes explaining a signficant portion of the total variance (Table 13 and 14).

The first CCA axis represents a gradient of zoo, size of item and number of items while the second CCA axis represents a gradient of color (Table 15). The color, size, durability, and number of enrichment items were more correlated with behaviors than the items' pliability or compressibility (Figure 4). Based on the CCA, higher frequencies of destructive, aggressive, and head cover behaviors were associated with larger items, while higher occurences of environment manipulation and displays were correlated with smaller items (Figure 4). Moreover, higher frequencies of abnormal and submissive behaviors were associated with larger numbers of sturdy, brightly colored items (Figure 4). Sexual behaviors were correlated with an increase in both the size and numbers of objects (Figure 4). The characteristics of items did not have an impact on the amount of time the orangutans spent manipulating the items (Table 16). There was no relationship between the behaviors and enrichment characteristics when in holding ($F_{1,23}$=1.266, P=0.230).

Discussion

A move towards greater naturalism in the design of zoo exhibits over the past four decades has had positive implications for the captive animal inhabitants as well as the zoo visitors [Lukas and Ross,

2014; Newberry, 1995; O'Neill et al., 1991; Price et al., 1994]. Within that context, however, the effectiveness of enrichment on animal behavior has yet to be systematically studied. Based on the overall composite behavioral repertoire of orangutans at two zoos, I found no differences in outcomes when non-natural versus natural enrichment items were offered. Given that adequate enrichment is provided in some fashion, this finding suggests that zoos should feel less constrained with regard to naturalistic-only enrichment policies on exhibit. Even so, it is important to consider the significant effects of the naturalistic properties on individual behaviors. The separate analyses of variance depicted that social behaviors were influenced by these categories more than solitary behaviors. Specifically, the use of non-natural items was associated with significantly higher frequencies of affiliative behaviors and conspecific approximation. Friendly social interaction is widely considered to be a favorable behavior amongst captive primates [Cheney et al., 1986; de Waal and van Roosmalen, 1979; Dunbar, 1991; Enciso et al., 1999; Flack et al., 2006], even in the semi-solitary orangutans [Edwards and Snowdon, 1980; Perkins, 1992; Poole, 1987]. In fact, the frequencies of all other social behaviors recorded (aggression, sexual, and submission) were higher with non-natural items, albeit these differences were not statistically significant. These results amplify past claims that social behaviors, whether favorable or adverse, are positively correlated with the inclusion of enrichment at large [Honess and Marin, 2006; Sha et al., 2012]. Though the naturalism of enrichment items did not impact the overall behavior composite of the orangutans, the results suggest that it can impact behaviors on an individual basis, so zoos should take such possibilities into consideration when implementing their enrichment program.

It is well established that the behavioral repertoires of captive apes can differ drastically between exhibit and holding facilities [Hoff et al., 1997; Lukas et al., 2003; Perkins, 1992; Ross et al., 2010]. In this case, the analyses did not indicate any effect on overall behavior repertoires or on individual behavior. Nonetheless, it is important to note that the orangutans were housed individually in

their holding stalls, meaning there was no opportunity for social interactions to occur and thus be impacted by enrichment category.

Finding higher frequencies of destructive and aggressive behaviors in association with larger items was not unexpected. Previous studies have shown that desirable enrichment objects increase intragroup aggression in apes [Bloomstrand et al., 1986; Tarou et al., 2004], and it is plausible that larger items were more appealing to the orangutans. A linear relationship between head cover behavior and enrichment item size was also fairly probable. Wild orangutans use large leaves, twigs, or tree bark to cover themselves in the wild [McConkey, 2005], and bigger items allow for more coverage. On the other hand, the higher frequencies of abnormal and submissive behaviors associated with larger numbers of items was not anticipated. The provisioning of enrichment is usually accompanied by a decrease in stereotypies [Baker, 1999; Newberry, 1995; Swaisgood and Shepherdson, 2005; Tripp, 1985], but too much enrichment can possibly overstimulate captive animals and induce abnormal behaviors [Wemelsfelder and Birke, 1997]. Overall, the frequency of abnormal behaviors within the study group was remarkably low, at < 1%. Because physical properties of provisioned enrichment can impact behavioral outcomes regardless of their naturalism, enrichment policies should place emphasis on the specific item properties instead of their perceived naturalism. As supported by other captive animal studies (Fragaszy and Adams-Curtis 1991; Renner and Seltzer, 1991; Swaisgood and Shepherdson, 2005), certain orangutan behaviors may be promoted or suppressed through the use of particular enrichment items.

The characteristics of items did not, however, impact the frequency of enrichment manipulation. Previous studies have both supported [Sambrook and Buchanan-Smith, 1996; Swaisgood et al., 2005] and refuted [Delfour and Beyer, 2011; Pruetz and Bloomsmith, 1992; Videan et al., 2005] this finding . As with most findings from such observational studies, these discrepancies may be attributed to substantial individual differences among the animals and/or institutional responses to

enrichment [Bloomsmith et al., 1990; Delfour and Beyer, 2011; Novak et al., 1993; Pruetz and Bloomsmith, 1992; Shepherdson et al., 2004; Videan et al., 2005]. Because of such contradictions, zoos should empirically assess the effectiveness of their enrichment programs and make appropriate adjustments on individual bases [Chamove & Anderson, 1989; Swaisgood and Shepherdson, 2005].

CONCLUSIONS

1. Overall behavioral composites of two groups of captive orangutans were not different between days given natural enrichment and days given non-natural enrichment items. However, it must be stressed that the exclusive provision of non-natural enrichment items did promote positively deemed behavior more than natural enrichment items.
2. Specific characteristics of enrichment items, regardless of their naturalism, affected the rates of both positively and negatively deemed behaviors. Thus, there is further support for the contention that the frequencies of individual behaviors may be promoted or suppressed with the use of certain enrichment items. For this reason, zoos should take the properties of enrichment items into consideration when designing enrichment programs, whatever the level of emphasis might be on naturalism within the exhibit.

ACKNOWLEDGMENTS

A special thank you to the keepers at the Fort Wayne Children's Zoo and the Louisville Zoo for their time and effort manipulating the enrichment items throughout the study. I would also like to thank the six assistants who skillfully helped with data collection, Dr. Gary Dodson for his guidance and support, and Jason Doll for his statistics assistance. This study was done in partial fulfillment of Master's degree requirements in the Department of Biology at Ball State University and was supported in part by the Ball State University Chapter of Sigma Xi and the Ball State Graduate ASPIRE Grant.

Literature Cited

Altmann J. 1974. Observational study of behavior: Sampling methods. Behav 48: 227-267.

Badihi I. 2006. The effects of complexity, choice and control on the behaviour and the welfare of captive common marmosets (*Callithrix jacchus*). [dissertation]. Stirling, UK: University of Stirling. p 411.

Baker KC. 1999. Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. Zoo Biol 16: 225-236.

Barbiers RB. 1985. Orangutans: Color preference for food items. Zoo Biol 4: 287-290.

Birke L. 2002. Effects of browse, human visitors and noise on the behavior of captive orangutans. Anim Welf 11: 189-202.

Bloomsmith MA, Brent LY, Schapiro SJ. 1991. Guidelines for developing and managing an environmental enrichment program for nonhuman primates. Lab Anim Sci 41: 372–377.

Bloomsmith MA, Finlay TW, Merhalski JJ, Maple TL. 1990. Rigid plastic balls as enrichment devices for captive chimpanzees. Lab Anim Sci 40: 319-322.

Bloomstrand MA, Riddle K, Alford P, Maple T. 1986. Objective evaluation of a behavioral enrichment device for captive chimps. Zoo Biol 5: 293-300.

Boere V. 2001. Environmental enrichment for Neotropical primates in captivity. Cienc Rural 31: 543-551.

Campbell S. 1984. A new zoo? Zoonooz 55: 4-7.

Carlstead K, Seidensticker J, Baldwin R. 1991. Environmental enrichment for zoo bears. Zoo Biol 10: 3-16.

Chamove AS, Anderson JR. 1989. Examining environmental enrichment. In: Segal EF, editor. Housing, care and psychological well-being of captive and laboratory primates. New Jersey, USA: Noyes Publications. p 183–199.

Cheney D, Seyfarth R, Smuts B. 1986. Social relationships and social cognition in nonhuman primates. Science 234: 1361-1366.

Coe JC. 1985. Design and perception: Making the zoo experience real. Zoo Biol 4: 197-208.

Coe JC, Maple T. 1984. Approaching Eden: a behavioral basis for great ape exhibits. AAZPA , 1984 Annual Conference Proceedings, American Association of Zoological Parks and Aquariums, Wheeling, WV, 117-128.

Delfour F, Beyer H. 2011. Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). Zoo Biol 31: 137-150.

de Waal FB, van Roosmalen A. 1979. Reconciliation and consolation among chimpanzees. Behav Ecol Sociobiol 5: 55-66.

Dunbar RIM. 1991. Functional significance of social grooming in primates. Folia Primatol *57*: 121-131.

Edwards SD, Snowdon CT. 1980. Social behavior of captive, group-living orangutans. Int J Primatol 1: 39-62.

Enciso AE, Calcagno JM, Gold KC. 1999. Social interactions between captive adult male and infant lowland gorillas: Implications regarding kin selection and zoo management. Zoo Biol 18: 53–62.

Fragaszy DM, Adams-Curtis LE. 1991. Environmental challenges in groups of capuchins. In: Box HO, editor. Primate responses to environmental change. London: Chapman & Hall. p 239-264.

Flack JC, Girvan M, de Waal FB, Krakauer DC. 2006. Policing stabilizes construction of social niches in primates. Nature 439*:* 426-429.

Gold KC. 1997: The conservation role of primate exhibits in the zoo. In: Wallis J, editor. Primate conservation: The role of zoological parks. Oregon: American Society of Primatology. p 43-62.

Hare V, Ripsky D, Battershill R, Bacon K, Hawk K, Swaisgood R. 2003. Giant Panda enrichment: Meeting everyone's needs. Zoo Biol 22: 401-416.

Hebert PL, Bard K. 2000. Orangutan use of vertical space in an innovative habitat. Zoo Biol 19: 239-251.

Hoff MP, Powell DM, Lukas KE, Maple TL. 1997. Individual and social behavior of lowland gorillas in outdoor exhibits compared with indoor holding areas. Appl Anim Behav Sci 54: 359-370.

Honess, PE, Marin CM. 2006. Enrichment and aggression in primates. Neurosci Biobehav Rev 30: 413-436.

Kreger MD, Hutchins M, Fascione N. 1998. Context, ethics, and environmental enrichment in zoo and aquariums. In: Shepherdson DJ, Mellen J, Hutchins M, editors. Second nature: Environmental enrichment for captive animals. Washington, DC: Smithsonian Institution Press.

Kutska, D. 2009. Variation in visitor perceptions of a polar bear enclosure based on the presence of natural vs un-natural enrichment items. Zoo Biol 28: 292-306.

Lukas KE, Ross S. 2014. Naturalistic exhibits may be more effective than traditional exhibits at improving zoo-visitor attitudes toward African Apes. Anthrozoos 27: 435-455.

Lukas KE, Hoff MP, Maple TL. 2003. Gorilla behavior in response to systematic alternation between zoo enclosures. Appl Anim Behav Sci 81: 367-386.

Maple TL. 1983. Environmental psychology and great ape reproduction. Int J Study Anim Probl 4: 295-299.

Maple TL, Perkins LA. 1996. Enclosure furnishings and structural environmental enrichment. In: Kleiman DG, editors. Wild mammals in captivity: Principles and techniques. Chicago: University of Chicago Press. p 212-223.

Maple TL, Stine W. 1982. Environmental variables and great ape husbandry. Am J Primatol 3: 67-76.

Mason G, Clubb R, Latham N, Vickery S. 2007. Why and how should we use environmental enrichment to tackle stereotypic behavior? .Appl Anim Behav Sci 102: 163-188.

McConkey, K. 2005. Sumatran orangutans. In: Caldecott C, Miles L, editors. World atlas of great apes and their conservation. Berkeley: University of California Press. p 456.

McPhee M. Foster JS, Sevenich M, Saunders CD. 1998. Public perceptions of behavioral enrichment: Assumptions gone awry. Zoo Biol 17: 525-534.

Moss A, Esson M, Francis D. 2010. Evaluation of a third-generation zoo exhibit in relation to visitor behavior and interpretation use. J Interpret Res 15: 11-28.

Newberry RC. 1995. Environmental enrichment: Increasing the biological relevance of captive environments. Appl Anim Behav Sci 44: 229-243.

Novak MA, Musante A, Munroe H, O'Neill PL, Price C, Suomi SJ. 1993. Old, socially housed rhesus monkeys manipulate objects. Zoo Biol 12: 285-298.

Oksanen J, et al. 2013.Vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

O'Neill PL, Novak MA, Suomi SJ. 1991. Normalizing laboratory-reared rhesus macaque *(Macaca mulatta*) behavior with exposure to complex outdoor enclosures. Zoo Biol 10: 237-245.

Perkins L. 1992. Variables that influence the activity of captive orangutans. Zoo Biol 1: 177-186.

Poole TB. 1987. Social behavior of a group of orangutans (*Pongo pygmaeus*) on an artificial island in Singapore Zoological Gardens. Zoo Biol 6: 315-330.

Price E, Ashmore L, McGiven A. 1994. Reactions of zoo visitors to free-ranging monkeys. Zoo Biol 13: 109-118.

Pruetz JD, Bloomsmith MA. 1992. Comparing two manipulable objects as enrichment for captive chimpanzees. Anim Welf 1: 127-137.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reade LS, Waran NK, 1996. The modern zoo: How do people perceive zoo animals? Appl Anim Behav Sci 47: 109-118.

Renner MJ, Seltzer CP. 1991. Molar characteristics of exploratory and investigatory behavior in the rat (*Rattus norvegicus*). J Comp Psychol 105: 326–339.

Ross SR, Wagner KE, Schapiro SJ, Hau J. 2010. Ape behavior in two alternating environments: Comparing exhibit and short-term holding areas. Am J Primatol 72: 951-959.

Ross SR, Wagner KE, Schapiro SJ, Hau J, Lukas KE 2011. Transfer and acclimatization effects on the behavior of two species of African great ape (*Pan troglodytes* and *Gorilla gorilla gorilla*) moved to a novel and naturalistic zoo environment. Int J Primatol 32: 99-117.

Sambrook TD, Buchanan-Smith HM. 1996. What makes novel objects enriching? A comparison of the qualities of control and complexity. Lab Primate Newslett 35: 1-4.

Sha J, Han S, Marlena D, Kee J. 2012. Effects of single-use and group-use Enrichment on stereotypy and intragroup aggressive and affiliative behaviors of a social group of squirrel monkeys at the Singapore Zoo. J Appl Anim Welf Sci 15: 358-371.

Shepherdson DJ. 2003. Environmental enrichment: Past, present and future. Int Zoo Yearb 38: 118-124.

Shepherdson D J, Carlstead KC, Wielebnowski N. 2004. Cross-institutional assessment of stress responses in zoo animals using longitudinal monitoring of faecal corticoids and behaviour. Anim Welf 13: 105-113.

Shettel-Neuber, J. 1988. Second and third generation zoo exhibits: A comparison of visitor, staff, and animal responses. Environ Behav 20: 452-473.

Swaisgood R, Shepherdson DJ. 2005. Scientific approaches to enrichment and stereotypies in zoo animals: What's been done and where should we go next? Zoo Biol 24: 499-518.

Swaisgood R, White AM, Zhou X. 2005. How Do Giant Pandas (*Ailuropoda melanoleuca)* Respond to varying properties of enrichments? A comparison of behavioral profiles among five enrichment items. J Comp Psychol 119: 325-334.

Swaisgood R, et al.2000. A quantitative assessment of the efficacy of an environmental enrichment programme for giant pandas. Anim Behav 61: 447-457.

Tarou LR, Kuhar CW, Adcock D, Bloomsmith MA, TL Maple. 2004. Computer-assisted enrichment for zoo-housed orangutans (*Pongo pygmaeus*). Anim Welf 13: 445-453.

Tripp JK. 1985. Increasing activity in captive orangutans: Provision of manipulable and edible materials. Zoo Biol 4: 225-234.

Videan EN, Fritz J, Schwandt ML, Smith HF, Howell S. 2005. Controllability in environmental enrichment for captive chimpanzees (*Pan troglodytes*). J Appl Anim Welf Sci 8: 117-130.

Wemelsfelder F, Birke L. 1997. Environmental challenge. In: Appleby MC, Hughes BO, editors. Animal Welfare. Wallingford, Oxon: CABI Publishing. p 35–47.

White BC, Houser LA, Fuller JA., Taylor S, Elliott JL. 2003. Activity-based exhibition of five mammalian species: Evaluation of behavioral changes. Zoo Biology *22*: 269-285.

Wilson S. 1982. Environmental influences on the activity of captive apes. Zoo Biol 1: 201-209.

Wright BW. 1995. Novel item enrichment program reduces lethargy in orangutans. Folia Primatol 65: 214-218.

Young RJ. 2003. Environmental enrichment for captive animals. Oxford, UK: Blackwell Science.

Table 1. Life history information of seven captive orangutans from two zoo populations.

Institution	Subject	Sex	Birth date	Birth/rearing	Species
Fort Wayne Children's Zoo	Tengku	M	7/3/1986	Captive	*Pongo abelii*
	Melati	F neutered	11/19/1984	Captive	hybrid
	Tara	F	4/1/1995	Captive	*Pongo abelii*
Louisville Zoo	Teak	M neutered	11/21/1987	Captive hand reared	hybrid
	Segundo	M	11/12/1987	Captive	*Pongo abelii*
	Amber	F neutered	10/15/1987	Captive hand reared	hybrid
	Bella	F	7/1/1984	Captive	*Pongo abelii*

Table 2. Characterization of enrichment items used to determine whether the naturalism of enrichment impacts captive orangutan behavior.

Naturalistic	**Non-naturalistic**
Browse	Paper products
Wood wool and other fiber	Blankets/sheets
Mulch/wood shavings	Plastics (heavy and light)
Straw/hay	Clothing items
Food enrichment (smears, scattered, pinecones, frozen treats)	Cardboard products
Water	Nylabones
Coconuts	Stuffed animals

Table 3. Behaviors deemed desirable and undesirable for captive orangutan.

Positive	**Negative**
Increase in overall activity	Stereotypies (repetitive behaviors, pacing, rocking, thumb-sucking, spinning, etc.)
Arboreal locomotion	Self-mutilation
Foraging	Excessive aggression
Nest building	Exhibit destruction
Head covering	Coprophagy/urophagy
Tool use	Regurgitation
Allogrooming	Excessive autogrooming

Table 4. The six properties used to analyze enrichment items and their corresponding criteria.

Property	**Category and Criteria**
Compressibility	Ability to compress material with one hand
	Soft- Compressible
	Hard-Not compressible
Pliability	Ability to bend material without breaking
	Low- not bendable with effort
	Medium- bendable with minimal effort
	High- bendable without effort
Durability	Ability to break/take apart
	Low- readily breakable
	Medium- possible to break/take part with effort
	High- not possible to break/take apart
Size	Small- ≤12in
	Medium- 13≤36in
	Large- >37in
Number	1
	2-5
	6-10
	≥11
Color	Neutral- tans, browns, grays, blacks, whites, dull greens and blues
	Non neutral- all other colors

Table 5. Complete ethogram used to monitor and record the behavior of seven captive orangutans. Modified from (Ross, 2011)

Behavior	**Modifier**	**Description**
Agonism		
Contact aggression	Recipient	Exhibiting aggressive physical contact including hitting, grabbing, scratching, biting, wrestling
Receive contact aggression	Actor	Receiving any of the above behaviors
Non-contact aggression	Recipient	Exhibiting aggressive behaviors with no physical contact including lunging, rushing, chasing, threats, baring teeth
Receive non-contact aggression	Actor	Receiving any of the above behaviors
Display	N/A	Portraying aggressive behavior without any clear recipient
Portrays submissive behavior	Recipient	Exhibiting submissive behaviors including crouching, displacing, avoidance, etc.
Receives submission	Actor	Receiving any of the above actions
Sexual		
Sexual examination	Recipient	Conducting any form of sexual examination including the use of touch (bodily or with the use of an outside item) or otherwise (visual, oral, or olfactory) to inspect the ano-genital region of self or another
Receives sexual exam	Actor	Receiving any of the above behaviors from another
Mount	Recipient	Initiating sexual contact (except sexual manipulation), including mounting, thrusting, and complete copulation
Receive mount	Actor	Receiving mount
Sexual present	Recipient	Presenting ano-genital region to another individual

Receive sexual present	Actor	Receiving the presentation of the ano-genital region of another individual
Masturbation	N/A	Actively using a body part, object, or environment to stimulate one's own genitals
Social		
Social play	Partner	Participating in friendly interactions involving two or more individuals including rolling, tumbling, wrestling, vigorous locomotion, tickling, chasing, biting, pulling, etc.; never accompanied by pilo-erection or agonism
Allogroom	Recipient	Picking at hair or skin of another individual and removing debris with hands, mouth, or object
Receive allogroom	Actor	Receiving social groom (see above)
Prosocial	Partner	Participating in social interactions outside the realm of aggression, play, or grooming, including touching, embraces, holding, and play solicitation.
Beg	Recipient	Sitting or standing within one meter of conspecific (usually possessing food or a desirable object), while staring at conspecific's face, mouth, hand, object, etc.
Receive beg	Actor	Receiving begging actions (see above) from another individual
Give food/ enrichment	Recipient	Voluntarily giving food or enrichment item to a conspecific
Take food/ enrichment	Original possessor	Taking food or enrichment item from another's mouth or hand
Receive food/enrichment	Giver	Receiving a food or enrichment item from a conspecific
People interaction	Visitor	Engaging in interaction with visitors across glass barrier, or attempting to interact with researcher
Keeper interaction	Keeper	Interacting with keeper through feeding, training, etc.
Solitary		
Eating/drinking	N/A	Consuming food items part of daily diet or water
Environment	N/A	Manipulating permanent structures within the closures

Destruction	N/A	Destructing an aspect of the permanent enclosure
Horizontal locomotion	N/A	Changing location in horizontal space by walking or running on a stable platform
Vertical locomotion	N/A	Changing location in vertical space by climbing, sliding, jumping, or moving on an unstable platform such as flexible ropes or wires
Brachiating	N/A	Progressing in movement by swinging from hold to hold by the arms
Attention	N/A	Directing attention to the holding areas, researchers, or visitors; face must be within 1 meter of separating glass or mesh
Auto grooming	N/A	Picking through own hair and skin
Scratch	N/A	Bringing fingers over the skin in long strokes
Self	N/A	Touching one's hands/feet to touch own body in the form of clapping, tapping, etc. (aside from head covering)
Head covering	N/A	Covering one's head with both hands or item
Aberrant	N/A	Exhibiting any behavior outside the realms of normal orangutan behavior, includes repetitive behaviors, pacing, rocking, thumb-sucking, spinning, regurgitation of food, coprophagy etc.
Self-mutilation	N/A	Exhibiting self-harming behaviors, including scab picking, excessive grooming, and hair plucking
Inactive	N/A	Not moving or active in any other behaviors below; eyes may be open or closed
Object manipulation		
Food item	N/A	Manipulating or examining a food item provided as part of daily diet that clearly does not include ingestion
Environment	N/A	Manipulating, examining, or destructing the physical environment including walls, trees, mulch, mesh, artificial vines, hanging ropes, etc.

Enrichment	N/A	Manipulating (aside from head covering) items that are supplementary and artificial objects added to the environment; specific item use will be noted
Nesting material	N/A	Manipulating items in the act of constructing or modifying nest site (limited to modification or immediate construction of nest itself, does not include gathering and carrying building materials)
Out of view	N/A	Individual's behavior is not able to be identified due to visual obstruction

Table 6. The subset used to monitor and record the proximity of orangutan conspecifics. Modified from (Ross, 2011)

Proximity	**Modifier**	**Description**
Contact	Contacted individual	Subject is touching another individual
Proximate	Neighbor	Subject (at center of mass) is within 1 m of another individual
Distant	None	Subject is more than 1 m from any other individual
Unknown proximity	None	It is impossible to determine the distance of the subject to its nearest neighbor

Table 7. Condensed ethogram of captive orangutan behaviors used for analysis.

Behavior	Description
Inactive	Not moving or active in any other behaviors, eyes may be open or closed
Attention	Directing attention to the holding areas, researchers, or visitors; face must be within 1 meter of separating glass or mesh
Object manipulation	Manipulating temporary enrichment items
Head cover	Using both hands or on object to cover head
Feed forage	Collecting, eating, or drinking daily diet
Self	Participating in self-directed behavior includes auto grooming, body tapping, hand clapping, etc.
Vertical locomotion	Changing location in the vertical plane or in arboreal fashion, includes brachiation and climbing.
Horizontal locomotion	Changing location in the horizontal plane, includes walking, running, etc.
Environment	Manipulating permanent structures within the closures
Scratch	Bringing fingers over the skin in long strokes
Abnormal	Engaging in behavior outside the realms of normal behavior, includes repetition, pacing, rocking, spinning, regurgitation, coprophagy, etc.
Destruction	Destructing an aspect of the permanent enclosure
Display	Expressing aggressive behavior without any clear recipient
People interaction	Attempting to or engaging in interaction with visitors or researchers
Proximity	Being within one yard of or in direct contact with a conspecific
Affiliative	Engaging in a positive interaction with a conspecific
Sexual	Partaking in sexual behavior, includes sexual examinations, sexual presentations, and copulation
Aggression	Demonstrating agonistic behavior (contact or non-contact) towards a conspecific
Submission	Expressing submissive behavior, includes crouching, displacing, and avoidance

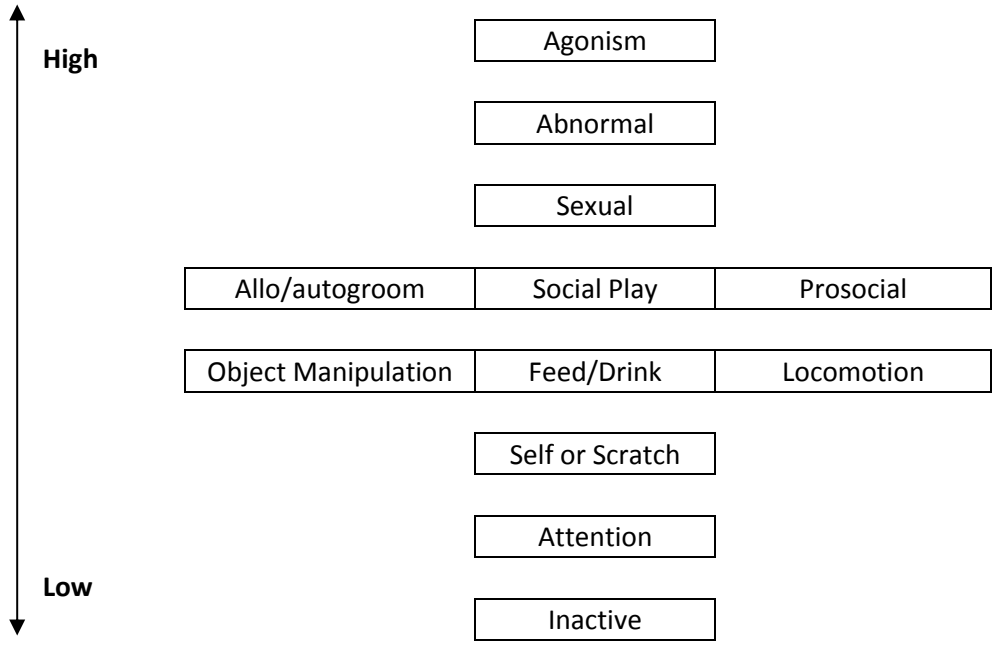

Figure 1. Behavioral tier diagram used in conjunction with the non-mutually exclusive ethogram. When more than one orangutan behavior occurred concurrently, the highest ranked behavior was recorded. If the exhibited behaviors were from the same tier, the more vigorous behavior was recorded.
Modified from (Ross, 2011)

Table 8. Comparison of the average percentages (SE) of captive orangutan behaviors observed on exhibit when given natural versus non-natural enrichment items. These behaviors reflect those used in MANCOVA.

	Mean Percent (SE)			
Behavior	Natural	Non-natural	*F*	*p*
Aggression	0.07 (0.06)	0.15 (0.08)	1.73	0.197
Sexual	0.49 (0.28)	0.51 (0.17)	0.78	0.385
Affiliative	2.49 (0.92)	5.13 (1.81)	5.17	*0.030
Submission	0.04 (0.02)	0.09 (0.06)	0.29	0.596
Feed forage	5.74 (0.80)	5.49 (0.93)	0.40	0.531
Object manipulation	10.44 (2.24)	13.06 (2.27)	1.63	0.211
Abnormal	0.82 (0.19)	0.51 (0.15)	1.97	0.170
Destruction	0.29 (0.15)	0.12 (0.07)	0.72	0.402
Attention	16.25 (2.44)	14.41 (1.52)	0.66	0.422
Vertical locomotion	6.18 (0.71)	6.31 (0.60)	0.05	0.833
Horizontal locomotion	3.19 (0.47)	2.37 (0.31)	2.83	0.102
Self	5.16 (1.32)	5.86 (1.31)	2.06	0.160
Scratch	0.93 (0.20)	1.06 (0.21)	0.46	0.504
Display	0.14 (0.08)	0.08 (0.04)	0.16	0.692
People interaction	0.70 (0.36)	0.37 (0.11)	0.22	0.641
Environment	2.94 (0.54)	2.30 (0.37)	0.80	0.378

* $p < 0.05$

Table 9. Comparison of the average percentages (SE) of captive orangutan behaviors observed on exhibit when given natural and non-natural enrichment items. These behaviors reflect those used in separate ANCOVAS.

	Mean Percent (SE)			
Behavior	Natural	Non-natural	*F*	*p*
Inactive	43.34 (3.21)	41.71 (3.45)	0.35	0.559
Head cover	2.14 (0.08)	10.73 (2.00)	10.02	*0.020
Proximity	7.69 (1.56)	13.24 (2.46)	4.23	*0.048
Time in possession	16.03 (3.35)	35.57 (6.80)	14.97	*<0.00
Tool use	0.07 (0.03)	0.06 (0.03)	0.02	0.884

* $p < 0.05$

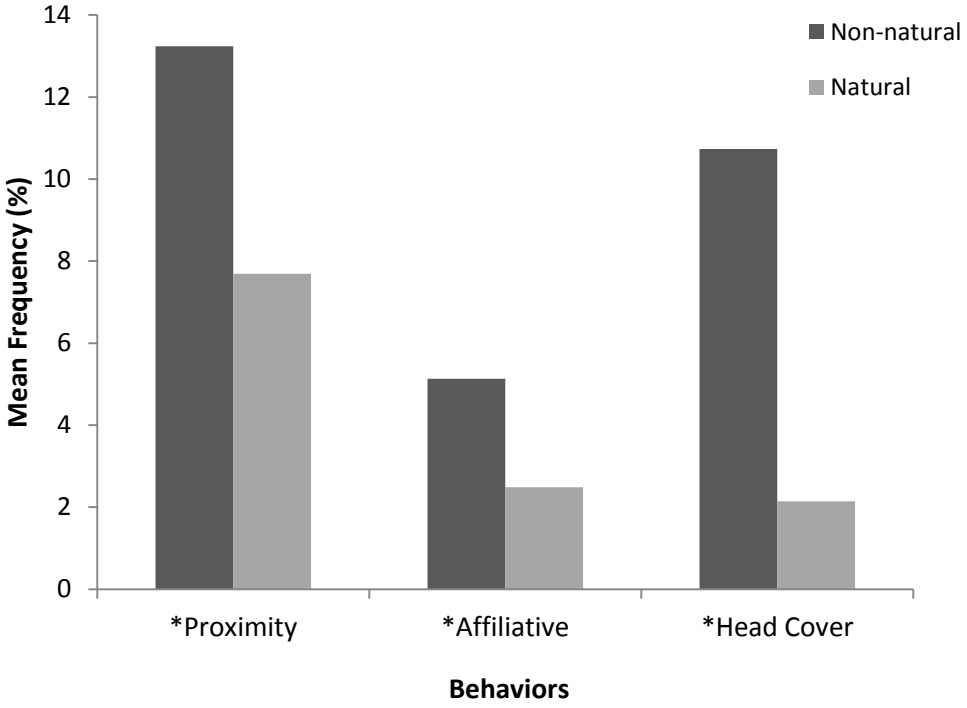

Figure 2. Mean percentage of time captive orangutans exhibited each behavior between natural and non-natural enrichment days [*P<0.05].

Table 10. Comparison of the average percentages (SE) of captive orangutan behaviors observed in holding when given natural versus non-natural enrichment items. These beviors reflect those used in MANCOVA.

	Mean Percent (SE)			
Behavior	Natural	Non-natural	*F*	*p*
Feed forage	10.44 (2.87)	10.47 (1.72)	0.02	0.887
Object manipulation	10.34 (1.83)	9.25 (4.59)	0.60	0.495
Abnormal	1.16 (4.65)	1.70 (1.53)	0.08	0.793
Attention	6.37 (1.89)	7.59 (2.62)	0.37	0.585
Vertical locomotion	2.72 (0.42)	3.77 (1.82)	0.18	0.696
Horizontal locomotion	1.73 (0.59)	1.74 (0.42)	0.13	0.740
Self	3.21 (2.78)	2.42 (1.27)	0.04	0.860
Scratch	1.74 (1.03)	0.95 (0.32)	0.17	0.709
Display	0.20 (0.09)	0.07 (0.07)	4.51	0.124
People interaction	2.77 (0.55)	3.80 (0.36)	2.15	0.239
Environment	6.60 (2.07)	4.52 (1.48)	4.89	0.114
Nest building	0.20 (0.08)	0.75 (0.39)	1.16	0.361

Table 11. Comparison of the average percentages (SE) of captive orangutan behaviors observed in holding when given natural and non-natural enrichment items. These behaviors reflect those used in separate ANCOVAS.

	Mean Percent (SE)			
Behavior	Natural	Non-natural	*F*	*p*
Inactive	51.88 (6.14)	51.61 (6.88)	0.08	0.984
Head cover	3.15 (2.98)	1.99 (1.27)	0.01	0.929
Time in possession	11.39 (2.22)	18.17 (7.67)	0.93	0.407
Tool use	0.11 (0.11)	0.79 (0.79)	1.00	0.391

Table 12. Comparison of the average percentages (SE) of time the captive orangutan spent within the 12 outline segments of each enclosure when given natural and non-natural enrichment items.

	Mean Percent (SE)			
Behavior	Natural	Non-natural	*F*	*p*
Left Up Front	2.61 (0.90)	3.88 (0.98)	3.07	0.089
Left Up Back	10.17 (2.05)	13.10 (3.07)	0.85	0.363
Left Down Front	3.39 (0.93)	3.21 (0.94)	0.02	0.884
Left Down Back	16.25 (2.23)	17.58 (2.46)	0.18	0.672
Middle Up Front	12.70 (2.95)	11.96 (2.55)	0.01	0.951
Middle Up Back	16.85 (2.90)	16.19 (2.22)	0.03	0.868
Middle Down Front	6.68 (1.49)	7.67 (2.61)	0.85	0.364
Middle Down Back	4.19 (0.86)	5.15 (1.39)	0.14	0.711
Right Up Front	5.11 (1.89)	4.89 (1.72)	0.10	0.755
Right Up Back	12.20 (2.42)	9.42 (2.25)	2.92	0.097
Right Down Front	3.97 (1.28)	2.57 (1.17)	1.45	0.236
Right Down Back	4.50 (1.15)	1.99 (0.51)	4.45	*0.043

* $p < 0.05$

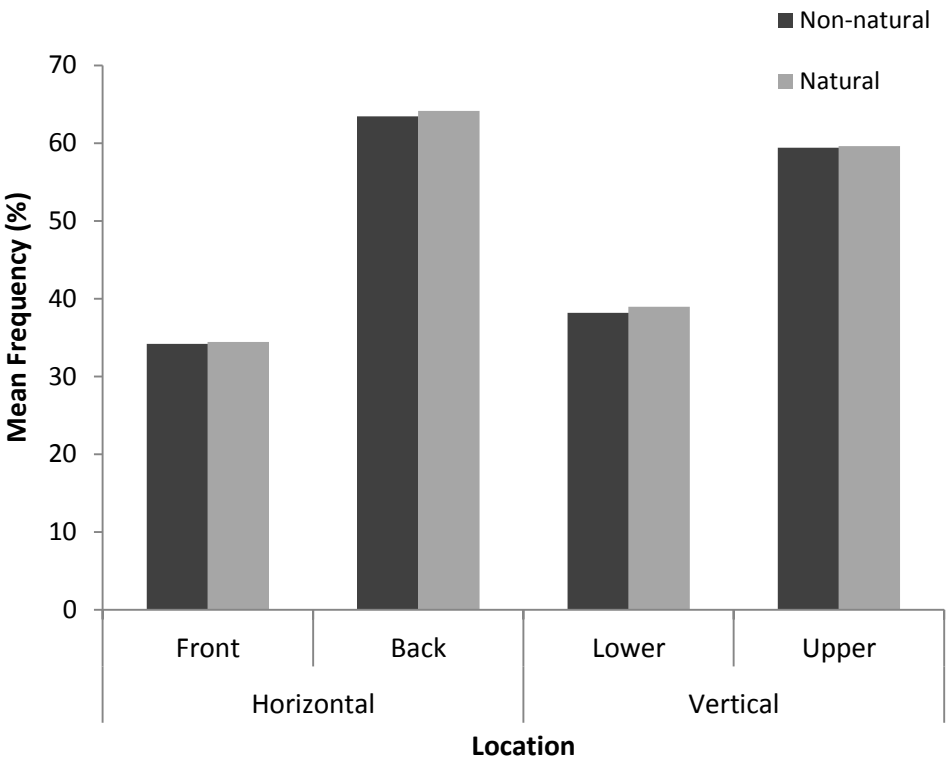

Figure 3. Space utilization of captive orangutans when given natural and non-natural enrichment. Front and back variables portray horizonal variation while lower and upper variables illustrate vertical variation.

Table 13. Results from the Canonical Correspondence Analysis (CCA) ANOVA permutation for the CCA evaluating the relationship between enrichment characteristics and observed captive orangutan behavior.

Axes	Df	Chi^2	*F*	N. permutation	*p*
CCA1	1	0.1893	23.653	199	0.005
CCA2	1	0.0736	9.197	199	0.005
CCA3	1	0.0510	6.373	399	0.022

Table 14. Accumulated constrained eigenvalues for the first, second, and third axes of the Canonical Correspondence Analysis (CCA) evaluating the relationship between enrichment characteristics and captive orangutan behavior. CCA eigenvalues represent the strength of the relationship between enrichment characteristics and behaviors. These values are tested against the null model of no relationship by using an ANOVA-like permutation.

	CCA1	CCA2	CCA3
Eigenvalue	0.1893	0.0736	0.0510
Proportion explained	0.5516	0.2145	0.1486
Cumulative proportion	0.5516	0.7660	0.9147

Table 15. Canonical Correspondence Analysis (CCA) summary statistics for enrichment item characteristics correlation with axes. The zoo variable is included to control for variation between the two zoo populations.

Variable	CCA1	CCA2	CCA3
Zoo	-0.9454	-0.1661	-0.0581
Compressibility	0.0233	0.0025	0.4828
Pliability	-0.0543	0.0304	-0.6944
Durability	0.2162	-0.2442	0.5959
Size	0.3530	0.2759	-0.5328
Color	0.0820	-0.8784	-0.1213
Number	0.3124	-0.2835	-0.5015

Table 16. Canonical Correspondence Analysis (CCA) summary statistics for behavior correlation with axes.

Variable	CCA1	CCA2	CCA3
Aggression	0.7232	0.4907	0.0818
Sexual	0.7376	-0.0173	-0.1100
Forage	-0.4561	0.0454	0.1954
Object	0.4198	-0.2579	-0.0132
Prosocial	-0.2833	-0.5097	-0.2471
Abnormal	0.7809	-0.8540	1.2000
Destruction	0.3633	0.6139	0.6261
Attention	-0.6150	-0.0130	-0.0649
Inactive	-0.3326	0.0842	0.1369
Vertical locomotion	-0.1746	0.2800	-0.1676
Horizontal locomotion	-0.5777	0.1366	0.0166
Head cover	0.7309	0.4742	-0.1695
Self	0.3212	0.3989	0.0818
Scratch	0.1129	0.0816	0.1189
Submission	0.9658	-0.9123	0.5276
Display	-0.8092	-0.1236	0.0001
Interaction	-0.2384	-0.2079	-0.3205
Proximity	0.1363	-0.3223	-0.4013
Environment	-0.7636	-0.1111	0.1704
Time	0.4373	0.2206	0.0020

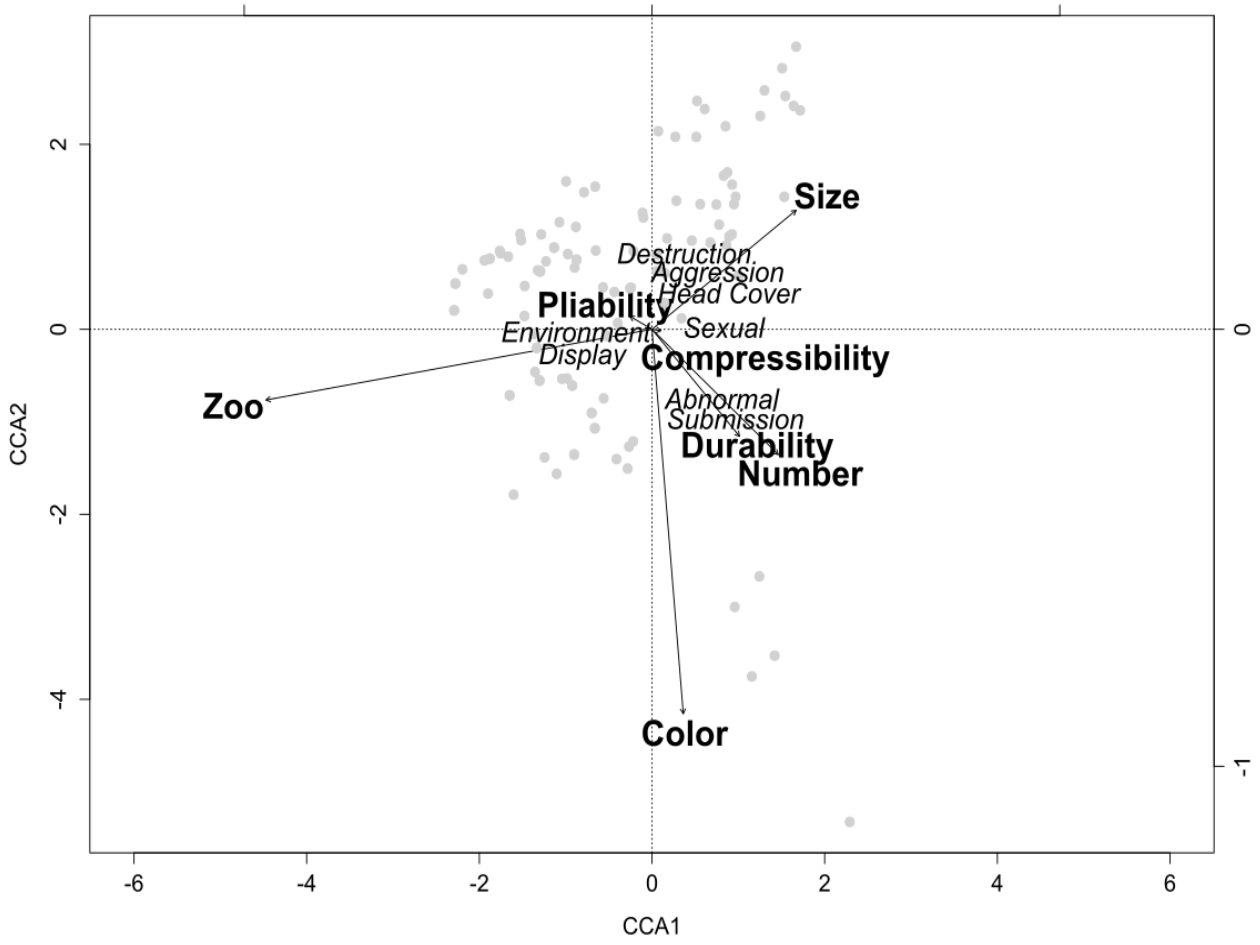

Figure 4: Canonical correspondence analysis biplot representing the relationship between five enrichment properties (arrows) and the four significantly impacted behaviors (italicized) during 112 observational days (dots). The lengths of arrows indicate the strength of significant correlation between the characteristics and behaviors. Axis One represents a gradient of zoo, size of item and number of items and Axis Two represents the gradient of color. Tables 15 and 16 include the numerical points for the characteristics and behaviors, respectively. The behaviors that were less impacted by the characteristics were left out to improve visual clarity.

Appendix

Public viewing area of the orangutan exhibit at the Fort Wayne Children's Zoo.

Inside the orangutan exhibit at the Fort Wayne Children's Zoo.

A view from the visitor's area into the indoor orangutan exhibit at the Louisville Zoo.

Inside the orangutan exhibit at the Louisville Zoo.