ORANGUTAN HEALTH AND BEHAVIOR:

IMPLICATIONS FOR NUTRITION IN CAPTIVITY

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by

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CHAPTER 1

INTRODUCTION

Species Introduction

Taxonomy and life history

In Malay, the language spoken in the countries where orangutans are found, the word "orangutan" literally translates to "person of the forest" (Knott, 1999). Orangutans are the only extant Asian great ape, inhabiting the Southeast Asian islands of Borneo and Sumatra. There are three recognized subspecies of orangutan**:** *Pongo pygmaeus abelii* (Bornean), *Pongo pygmaeus pygmaeus* (Sumatran), and the recently discovered *Pongo tapanuliensis* (Tapanuli). Largely due to habitat loss and exotic pet trade, all three groups are endangered (*The IUCN Red List of Threatened Species*, 2017). In a synthesis of previous population studies, Sugardjito (1995) put forth total population estimates ranging from 4,000 to as high as 145,000 total individuals. However, the World Wildlife Fund currently classifies Bornean orangutans as "Endangered", estimating 104,700 individuals in the wild, and Sumatran and Tapanuli groups as "Critically Endangered", with 14,613 and 800 individuals in the wild, respectively (Jayasinghe, WWF). The Tapanuli orangutan is currently the most critically endangered of any great ape species.

Phenotypically, the three subspecies differ in features such as cranial morphology, length, color, and structure of hair, the size and shape of male secondary sexual features, and the thickness of dental enamel (Courtenay et al., 1988; Goossens et al., 2009; Nater et al., 2017;

Smith et al., 2012). They also have such different genetic profiles that some researchers contend they represent entirely separate species (Nater et al., 2017; Xu & Arnason, 1996)**.** However, their behavioral similarities and ability to interbreed and produce viable offspring support maintaining the taxonomic designation at the subspecies level (Muir et al., 1998).

Fossil evidence provides clues about the evolution of extant orangutans. In a review of fossil relationships to extant primates, Harrison & Chivers (2007) noted that *Lufengpithecus, Sivapithecus*, and *Khoratpithecus* are all proposed ancestors of modern orangutans. All had marked sexual dimorphism, and *Lufengpithecus* and *Sivapithecus* reportedly had greater dimorphism than any extant primate (Harrison & Chivers, 2007; Kelley & Qinghua, 1991). This evidence suggests a historically polygamous social structure, and aligns with both the marked sexual dimorphism and the lack of monogamy or polyandry in modern populations (Harrison & Chivers, 2007). Although there was an abundant population of apes during the Miocene, modern orangutans are the only living descendants of ancestors of that diverged from the African apes between 10-16 million years ago (Cacconei & Powell, 1989; Conroy, 1990). The orangutan lineage further split into one group living in Batang Toru, an ecosystem that encompasses three districts in Tapanuli, Sumatra (Roshetko et al., 2007), and another living north of Lake Toba, approximately 3.4 million years ago. The Batang Toru group would become the Tapanuli group, and the other diverged again around 674,000 years ago to create the modern Bornean and Sumatran groups (Nater et al., 2017).

The divergence date of the orangutan lineage from that of the African apes is estimated to be 5 million years earlier than the divergence of African apes from the human lineage. This means that African apes and humans are more closely related to each other than either group is to orangutans (Conroy, 1990). Unique variables in the orangutan lifestyle, for example their arborealism, make this distinction clear. Extant orangutans live in in the treetops of various rainforest habitats that range from sea-level swamps and to mountain slopes (Knott, 1999). Population densities tend to decrease with increasing altitude, likely because the availability of their dietary staple of soft fruit also decreases at higher altitudes (Delgado & Van Schaik, 2000).

Body size for adult males and females averages 86.3 kg and 38.5 kg, respectively (Markham & Grows, 1990), making orangutans the largest tree-dwelling animals, and they display one of the highest degrees of sexual dimorphism among all primates. Sexually mature males are also unique among mammals because they have two morphotypes: those who have developed secondary sexual characteristics including large throat pouches to produce long calls, and jutting cheek pads (“developed” males), and those who remain smaller and without secondary sexual characteristics (“undeveloped” males) (Knott, 1999). The existence of two morphotypes for male orangutans is thought to be related to unique life history variables that increase reproductive success for non-alpha males, as discussed below.

Social structure

Beyond the consensus view that orangutans are semi-solitary, little is known about their true social system. Orangutans will sometimes go entire days without any social contact (Morrogh-Bernard et al., 2009) and most instances of social grouping are temporary – for mating or due to the fruiting of closely packed trees (Knott, 1999). One field study reported some grouping among females, particularly adolescents, but noted that nearly all male social interactions were exclusively for mating with females. The infrequent male/male interactions were always either avoidant or aggressive (Galdikas, 1985). This infrequency of social contact may contribute to the reproductive success of “undeveloped” males, as it makes it easier to sneak matings without being detected by dominant males (Harrison & Chivers, 2007).

Increased brain size relative to body size (and subsequently, increased complexity in sociality) are both hallmarks of extant diurnal primates, and quantifying the related encephalization may be an indicator of intelligence (Williams, 2002). If orangutan sociality aligned with that of other great apes, their intelligence would be suggestive of large social groupings rather than their unique semi-solitary structure. To explain this unexpected phenomenon, Knott (1999) proposed that the social differences may be due to ecological variation in feeding behavior.

It has been suggested that the fruit trees where orangutans spend a significant portion of their time feeding are much smaller than those fed from by chimpanzees and bonobos (Knott, 1999). Additionally, orangutans have evolved to eat very high-quality foods (Milton, 2003) that, due to environmental constraints, can be quite scarce (the specifics of these constraints will be discussed in later sections). When this inherent competition is considered in conjunction with their large body size, it follows that, unlike chimpanzees and bonobos, there is simply not enough fruit in single locations to allow for orangutan group foraging (Knott, 1999). Consequently, this may impede the ability for frequent social interactions.

Diet and phenotypic effects of feeding ecology

Orangutans are primarily frugivorous, with 61-71% of foraging time spent eating fruit (Bastian et al., 2010). Interestingly**,** their rainforest homes undergo unique “mast fruiting” events every 2-10 years, during which many of the rainforest trees fruit in synchrony (Ashton et al., 1988). The availability of fruit in orangutans' habitat is in a regular state of fluctuation, and the animals must adjust their feeding behavior accordingly. During the times of highest fruit production, orangutans display their preference for frugivory by eating a diet consisting exclusively of fruit. When fruit availability is low, their diet will contain as little as 21% fruit (Knott, 1998). When necessary, they will rely heavily on their fallback foods, including up to 37% bark as well as flowers, insects, leaves, and other vegetation (Bastian, et al., 2010; Knott, 1998; Knott, 1999). This is in contrast to the African apes' response to low-fruit periods, as gorillas and bonobos tend to feed largely on terrestrial herbaceous vegetation, while chimpanzees tend to disperse to lessen the pressure on fruit patches (Conklin-Brittain et al., 2001). In calculating overall activity budget, Delgado and Van Schaik (2000) reported averages across several studies that showed that orangutans spend about 43% of their time feeding, 41.5% resting, 13.5% traveling, and 2% in other activities such as nest-building, socializing, and mating. However, these values show substantial inter-individual variability because orangutans are relatively solitary (Knott, 1999).

Orangutans have the longest interbirth interval of any extant primate species, which may be due to their unique dedication to frugivory combined with their large body size (Galdikas & Wood, 1990; Knott, 1999; Wich et al., 2004) Wild female orangutans have lower estrogen levels during fruit-scarce periods, potentially reducing fertility (Knott, 1998). Thus, the sporadic nature of fruit abundance may contribute to the lengthy interbirth interval (Knott, 1999).

The orangutan post-cranium is adapted for a specialized form of arboreal locomotion called "quadrumanous scrambling", or using all four hands and feet to grasp and pull themselves along. Morphological characters associated with this type of locomotion are long forelimbs, hands with short thumbs, short hindlimbs with hand-like feet, and shallow hip joints that allow them to rotate their legs by more than 90 degrees. Together, these features create a unique ability to contort the body, making for easier navigation through the rainforest canopy and reaching of difficult to access fruit (Delgado & Van Schaik, 2000; Knott, 1999).

Orangutans in Captivity

Overview

Zoos play a particularly important role in the future of orangutans due to their dwindling populations in the wild. Not only do zoos provide opportunities for researchers to work more closely with the animals than is possible in the field, but through breeding programs and public education, they also serve an important role in conservation (Gippoliti, 2000). Despite these benefits, the lifestyle of captive animals differs significantly from their counterparts in the wild. In their native habitats, orangutans normally spend many hours a day foraging for foods (Bastian et al., 2010). This contrasts sharply with the more sedentary lifestyle in captivity. As will be discussed in later sections, this altered lifestyle, along with differences in diet, may play a role in the pervasive health issues and behavioral abnormalities common of captive orangutans (Cassella et al., 2012; Less et al., 2013a, 2013b).

Wild vs. Captive Diets

Notable differences between wild and captive orangutan health and behavior may be related to diet. As outlined above, wild orangutans spend nearly half of their active time feeding on as much fruit as is available, but the availability of fruit is highly variable. Due to this variability, it is difficult to assess the exact nutrition of the wild diet, and this complicates the question of how to provide food in a captive setting. It is difficult to know which season is best to mimic, and whether the variability itself is a healthy pattern. As such, most zoos use a standardized food product that, when supplemented with commercial fruits and vegetables, is intended to provide essential nutrients and calories to all captive primates (hereafter, “biscuits”).

However, the biscuit-based diet differs from wild feeding ecology in several important ways – it does not fluctuate in calories or nutritional content throughout the year, and it can be eaten quickly with little foraging. Further, the fiber content of the biscuit may not be sufficient. It is important to consider fiber content when developing a captive orangutan diet, as the wild diet consists largely of fiber (levels fluctuate between 24.1 – 60.8%) (Schmidt, D., 2004), and orangutans rely on fiber fermentation for a substantial portion of their energy (Schmidt, D.A. et al., 2005). There is a low-starch variety of biscuit, but it still promotes a higher-starch and lower-fiber diet than the wild would provide. Similarly, the fruits available locally are much higher in sugar and starch than those found in orangutans’ natural habitats. Zoo keepers attempt to provide food in such a way that is challenging and encourages foraging, but the captive diet is still much more readily accessible than the wild diet.

These factors, combined with (1) biscuits are formulated for human standards, and (2) the content is not tailored to individual primate species (Cassella, 2012), suggest that this well-intended diet may not be the healthiest choice for captive orangutans. It cannot mimic their natural nutrition and feeding patterns and, thus, differs from what they have evolved to eat in crucial ways. These problems may be contributing to the differences between wild and captive lifestyle variables.

Energy expenditure

Orangutans use less energy relative to body mass than any other placental mammal, including sedentary humans (Pontzer et al., 2010). Such low energy expenditure is unique in primates but is logical considering orangutans' slow growth rate and interbirth intervals. This low energy expenditure may be an evolutionary consequence of the variable food availability in Borneo and Sumatra (Pontzer et al., 2010). Ketones, evidence of fat catabolism, are present in orangutan urine only during low-fruit periods, indicating that they likely store fat for use in times of low food availability (Knott, 1998).

This finding is consistent with James Neel's "Thrifty Genotype Hypothesis" (1962), which describes a historic genotype that reinforced efficient intake/utilization of food in times of low availability. While useful in "the feast-or-famine days" (Neel, 1962), this compensatory mechanism is likely connected to the obesity and high frequency of diabetes common of modern human societies where food is readily available. The described compensatory tendency to store fat in humans is reflected in orangutan ketone analysis (Knott, 1998), and the food availability of civilized human societies is reflected in the characteristics of their captive diet. As such, orangutans may be facing a similar pattern wherein an evolutionary advantage becomes harmful in the face of environmental changes. Their captive lives are characterized by little need to forage for diets that do not fluctuate calorically or nutritionally, and a "thrifty" genotype may cause this pattern to lead to overweight captive animals.

The captive feeding schedule may contribute to a sedentary lifestyle that leads to health problems, or the diet itself may influence physiology in a way that promotes a lethargic lifestyle. In either case, diet and its presentation influence both physiology and behavior, and diet is an independent variable that can be experimentally manipulated. Experimentally altering the captive diet to more accurately mimic the nutritional makeup of wild diets (less starch, more fiber) will shed more light on the role that diet plays in the health problems and behavioral abnormalities that arise in captivity.

Implications for Behavior

Activity

Orangutans in the wild spend much of their time traveling, foraging, and feeding, so it is important to encourage activity in their captive environments. While zoo keepers do work to create novel feeding challenges and encourage the animals to explore their environment, activity levels in captivity do not fully mimic the wild. The introduction of novel enrichment items and environmental manipulation have been shown to increase activity levels (Hebert & Bard, 2000; Schrier et al., 2008). Furthermore, the number of animals, number of movable objects, amount of habitable surface area, and enclosure volume was, collectively, the best predictor of activity levels across nine captive environments (Perkins, 1992). Thus, large enclosures that contain maximum movable objects and social opportunities best promote increased activity. These findings support the hypothesis that current captive environments may be lacking in sufficiently stimulating environments. Providing novel objects and environments to increase activity levels may lead to weight loss and be beneficial to overall health.

Arboreality

As orangutans are primarily arboreal in the wild, encouraging arboreality in captivity is also an important concern, and a valuable form of enrichment (Herbert & Bard, 2000). Captive orangutans are relatively inactive and tend to remain on the lower levels of their enclosures (Schrier et al., 2008; Gippoliti, 2000; Wright, 1995), and few studies have looked particularly at increasing time spent elevated. In one case, flooding the enclosure floor did encourage use of higher space (Hebert & Bard, 2000).

Undesirable behaviors

Beyond activity levels and space use, it is also of value to investigate the occurrence of regurgitation and reingestion (henceforth, R/R). R/R is a behavior unique to captive non-human primates (Akers & Schildkraut, 1985), and is defined as "forceful and voluntary ejection of vomitus material out of the stomach which is then re-ingested". This is different from vomiting because the action is controlled and voluntary (Robbins, Orangutan SSP), and differed from rumination in herbivores because the anatomy of primates does not include R/R as a part of the usual digestive process (Hill, 2009). R/R is a poorly understood behavior, and hypotheses for its cause range from strictly dietary to strictly environmental. Some speculative causes include the feeding of sweet foods or high sugar/low fiber foods meant for human consumption, lack of high-fiber foods, lack of foraging opportunities, social deficits in early development, restricted living areas, boredom, stress, and anxiety (Gould & Bres, 1986; Robbins, Orangutan SSP).

In one New Zealand zoo, R/R in orangutans was as frequent as 22% of the daily activity budget, with bouts occurring multiple times a day and after nearly every meal (Robbins, Orangutan SSP). R/R has been shown to be influenced by diet. Implementing a low-starch, biscuit free diet either reduced or eliminated the behavior in gorillas, and modeling wild feeding behavior by giving daily browse and increasing foraging opportunities reduced R/R in one captive chimpanzee (Less et al., 2013a; Struck et al., 2007). Similarly, the presence of fresh browse predicted a decrease of R/R in orangutans (Cassella et al., 2012).

Coprophagy, or the deliberate consumption of feces, has been observed in conjunction with R/R (Hill, 2009; Hopper et al., 2016). This behavior is not unheard of in the wild, and may actually be an adaptive feeding strategy for bonobos (Sakamaki, 2010). However, as it is more common in captivity and has been noted to decrease with increased enrichment (Crosby & Dodson, 2015), it is also valuable to monitor the occurrence of coprophagy during any study of abnormal captive behaviors.

Implications for Health

Obesity and metabolic syndrome

The captive diet of readily available, high-calorie biscuits draws a parallel to the decreased activity, increased food intake, and change in food quality common of industrialized human societies. As great apes are the closest living genetic relatives of humans, it is not surprising that this westernized lifestyle is linked to some human-like health issues. Namely, these characteristics are linked to obesity, or an excessive amount of body fat in relation to lean body mass, in both groups (Less, 2012; Schmidt et al., 2006; Zimmermann et al., 2011). Obesity is independently problematic, but also heightens the risk of other diseases including atherosclerosis, inflammation, and type 2 diabetes (Dandona et al., 2004; Varki et al., 2009).

When several of the characteristics of obesity are present simultaneously, they can manifest into metabolic syndrome. Metabolic syndrome is defined as a cluster of the following six components: abdominal obesity, insulin resistance, elevated triglycerides, low levels of high-density lipoproteins, proinflammatory state, prothrombotic state, and elevated blood pressure (Grundy et al., 2004). Metabolic syndrome is often present in obese humans (Mathus-Vliegen, 2012). At present, there is no reliable way to confirm obesity in orangutans, but captive orangutans do tend to be heavier than their wild counterparts (Markham & Grows, 1990; Schrier et al., 2008).

Inflammation

Inflammation is a natural response to injury or infection that is critical for tissue repair (Schäffer et al., 1998), but long-term, metabolically-triggered inflammation is problematic and can exacerbate disease risks (Hotamisligil, 2006). Obesity is related to a state of chronic inflammation, as demonstrated by the analogous increase of circulating inflammatory markers and expansion of adipose tissue (Trayhurn & Wood, 2005). As such, inflammatory markers are a useful measure of obesity and metabolic health.

Upper Respiratory Tract Disease

The upper respiratory tract of primates consists of the nose, larynx, and trachea. Orangutans have well-developed sinuses and laryngeal air sacs compared to other great apes (Steinmetz & Zimmermann, 2011). As such, they are particularly susceptible to upper respiratory tract disease (URTD), specifically in the forms of sinusitis and airsacculitis (Ihms et al., 2016). This is a common problem in captivity, and may be associated with obesity and increased levels of systemic inflammatory markers (Gan at al., 2004; Lawson et al., 2006; O'Donnell et al., 2000).

URTD affects Bornean orangutans significantly more often than Sumatrans, and while it is most common is captivity, it has also been observed in orangutans in a natural Bornean environment (Zimmermann et al., 2011). The rarity of URTD in free-ranging orangutans suggests that the fecal contamination unique to captive enclosures may be a source of exposure to the disease (Cambre et al., 1980; Zimmermann et al., 2011). Thus, enclosures that better promote arboreality may help reduce the frequency of infections, as reducing ground time would lessen the fecal contact that can increase URTD (Gippoliti et al., 2000).

Heart disease

Obesity and increased baseline inflammation are also thought to play a role in the progression and pathogenesis of many diseases, including atherosclerosis and cardiovascular disease (Obanda et al., 2014). Data from chimpanzees have supported this relationship, showing that body weight does have significant influence on the occurrence of heart disease in apes. Obanda (2014) found that heart disease is more common in older individuals compared to younger, and an increased body weight exacerbates the risk. Further, increased levels of the inflammatory hormone C-reactive protein denote increased heart disease risk, further pointing to the conclusion that chronic inflammation is a factor in cardiovascular issues (Varki et al., 2009).

Most human heart disease is caused by coronary artery atherosclerosis, or hardening of the arteries within the walls of the heart (Varki et al., 2009). Conversely, heart issues in apes are more typically driven by myocardial fibrosis, which occurs in the absence of arterial obstruction (Lowenstine et al., 2016; Murphy & Dennis, 2011; Varki et al., 2009). Varki (2009) found that chimpanzees do not tend to experience human-like cardiac events (also known as heart attacks). While human heart attacks are triggered by coronary thrombosis, heart attacks in chimpanzees are due to arrhythmias triggered by their characteristic fibrosis. The pathology of heart disease in gorillas and orangutans is more like that of chimps than humans (Varki et al., 2009).

Despite this difference in pathology, heart disease is still the leading cause of mortality in captive apes, with one report that cardiac disease accounts for death in about 45% of bonobos, 41% of gorillas (it is the leading cause of death for adult male gorillas in zoos), 20% of orangutans, 38% of zoo chimpanzees, and 50% of colony chimpanzees. As such, heart disease should be considered during any study of captive health (Lowenstine et al., 2016; Murphy & Dennis, 2011).

Insulin resistance and type II diabetes

In a healthy person, the increase of circulating glucose that occurs after a meal prompts insulin release from beta cells in the pancreas. Insulin acts to regulate blood sugar by triggering either glucose uptake or storage, depending on the body's needs. In states of hypoglycemia, insulin prompts immediate uptake and use of the glucose. In states of hyperglycemia, it prompts storage of glucose in the liver for use during later hypoglycemic periods (Hall, 2016).

Poor diet can disrupt insulin regulation and cause the development of insulin resistance, which is characterized by a decrease in sensitivity to the effects of insulin and, thus, increased production of pro-inflammatory cytokines (Benítez-P Aez et al., 2016). If an individual develops insulin resistance, the body still produces insulin but tissues do not appropriately respond with the uptake and utilization of glucose (Xu et al., 2003). When the pancreas continues to produce insulin, but cells do not respond with the appropriate glucose regulation, the resistant state can progress into type II diabetes (Kuhar et al., 2013). This condition is relatively common in captive primates, likely in connection with their high-calorie diet and low-activity behavior patterns (Kuhar et al., 2013). Type II diabetes has been diagnosed in captive orangutans based on fasting insulin and glucose levels, and these levels can be improved through an increase in dietary fiber (Benítez-P Aez et al., 2016; Gresl et al., 2000; Lowenstine et al., 2016)

Effect of diet

The low-fiber, high-starch content of the captive diet likely contributes heavily to these issues. A diet high in simple carbohydrates is associated with both obesity and the incidence of heart disease, and a high-fiber diet may be protective against these risks (Anderson et al., 1994; Less et al., 2013b). Data from humans have shown that adequate fiber consumption is inversely related to inflammatory markers, body weight, body fat, and body mass index (Slavin, 2005; Weickert & Pfeiffer, 2008). Further, fiber consumption is a better predictor of cardiovascular disease risk factors than fat consumption (Ludwig et al., 1999). Cassella (2012) synthesized the issues of captive vs. wild diet discrepancy, obesity, and inactivity by implementing a reduced-biscuit diet that encouraged weight loss. She found that, after losing weight, the orangutans' amount of time spent locomoting tripled, and they spent more time occupying the highest levels of their enclosure. There was also a group trend toward reduced time spent on the ground (Cassella, 2012).

Serum biomarkers

Serum biomarkers are indicators of inflammation, metabolism, and obesity at the time of blood collection. Data from humans show that metabolic measures can predict cardiovascular disease (Laws & Reaven, 1992), and data from orangutans link chronic inflammation to the occurrence of airsacculitis (Lawson et al., 2006). By recording levels over time and during different diets, information can be gathered about the progression of disease state, and the influence of nutrition on health. Using these biomarkers to further investigate the relationship between disease and diet may help improve the health and longevity of captive orangutans. Biomarkers that are validated for use in non-human primates include:

Triglycerides

Triglycerides are fatty acids that serve as an energy source, but excess levels are associated with obesity and heart disease (Less, 2012). Humans who report low physical activity levels have markedly higher triglycerides than their more active counterparts, and higher triglyceride levels do positively correlate with BMI in female chimpanzees (Videan et al., 2007). High triglyceride levels are associated with heart disease and, often, myocardial infarction in longitudinal human studies (Carlson & Böttiger, 1972; Laws & Reaven, 1992), but high-fiber foods have been shown to lower triglyceride levels and protect against heart disease (Anderson, 1985). As orangutans living in captivity do tend to have higher concentrations of triglycerides than those in the wild, it will be valuable to monitor triglycerides during a transition to a higher-fiber diet (Schmidt et al., 2006).

Cholesterol

There are two types of cholesterol: low-density lipoprotein (LDL) and high-density lipoprotein (HDL) cholesterol, referring to the types of proteins that move them through the body. LDL is regarded as "bad cholesterol", as high levels are an indicator of heart disease in humans. HDL has an inverse relationship with heart disease, and may actually be protective (Gordon et al., 1977). In a longitudinal study of ischemic heart disease in humans, triglycerides and LDL cholesterol were direct indicators of heart disease risk independently, and an increase in both compounded that risk (Larsson et al., 1984). Total cholesterol is a less precise measure than examining LDL and HDL cholesterol independently (Gordon et al., 1977). Despite this, total cholesterol is also related to increased coronary heart disease mortality in humans (Verschuren et al., 1995). Both captive orangutans and gorillas do have higher levels of total cholesterol than their wild counterparts (Schmidt et al., 2006), and humans can have lower total and LDL cholesterol levels on high-fiber diets (Brown et al., 1999; Schmidt et al., 2006). Thus, despite heart disease appearing in different forms between humans and non-human primates, it will be useful to monitor orangutan total cholesterol during the transition to a higher-fiber diet (Less, 2012; Varki et al., 2009).

Insulin and glucose

Due to the impaired insulin response in insulin resistant and type II diabetic states (described above), both insulin and glucose continue to circulate in the blood stream of affected individuals (Less, 2012). There is growing evidence that insulin resistance is related to the chronic inflammation caused by obesity, and that a high-fiber diet can remedy insulin dysfunction (Ma et al., 2008; Weickert & Pfeiffer, 2008; H. Xu et al., 2003). As such, levels of circulating insulin and glucose may be useful indicators of obesity and inflammation, and predictors of inflammatory disease. Levels of circulating insulin and glucose are independently valuable in studies of metabolic health, but the ratio of insulin to glucose may be particularly useful in studies of obesity and diabetes (Kalra et al., 2015; Kuhl & Holst, 1976). A higher insulin to glucose ratio is related to weight gain and hypoglycemia, while a reduction is related to weight loss (Kalra & Gupta, 2016).

Leptin

Leptin is a hormone produced by adipose tissue that indicates body state and regulates energy balance by acting on feeding behavior (Shah & Braverman, 2012). When organisms are food deprived, leptin decreases, interacting with receptors in the hypothalamus to initiate hunger and promote feeding behavior (Kolaczynski et al., 1996). Conversely, when the organism has sufficiently eaten or overeaten, leptin promotes satiation and inhibits eating (O’Donnell et al., 2000).

In obese individuals, as the leptin transport proteins become saturated, it begins to circulate freely (O’Donnell et al., 2000). Thus, its relation to obesity and inflammation suggest that levels of circulating leptin may be useful in studies of obesity and inflammatory diseases (Trayhurn & Wood, 2005). Leptin levels do accurately reflect body mass, and have been shown to enhance the precision of body mass index (BMI) in estimating obesity in humans (Shah & Braverman, 2012). However, it is important to note whether an individual has type II diabetes before using leptin as an indicator of obesity, as this relationship between leptin and BMI does not exist in a disease state (Tatti et al., 2001).

The Current Project

Sedentary lifestyle and high starch/low fiber diets are associated with obesity and metabolic disorders in humans and captive great apes. Transition to a more high-fiber diet has been shown to increase activity in orangutans (Cassella, 2012) and eliminate behavioral abnormalities in gorillas (Less, 2012). To further investigate this relationship, the present study will carry out a similar diet manipulation with a population of Bornean orangutans housed at the Cleveland Metroparks Zoo. Health and behavioral data will be collected throughout the study period. This population includes three adults and one juvenile, all of whom were on a biscuit-based diet prior to manipulation.

This study will not attempt to mimic the content of wild diet, but rather, to match its nutritional makeup. Thus, the plan is to increase fiber by reducing fruit and increasing vegetables with a focus on fibrous leafy greens, provide regular browse, and eliminate biscuits from the diet entirely. Data collection will include awake blood samples to monitor the above-described obesity and inflammatory markers, and the use of an ethogram focused on time spent feeding, activity levels, and undesirable behaviors to track feeding behavior, general activity, space use, and R/R.

Hypotheses of this study include (1) time spent feeding will increase, (2) this will lead to increased active time, a more diverse space use pattern, and decreased undesirable behaviors, and

(3) inflammatory, obesity, and metabolism markers will improve – potentially indicating a healthier weight, and lowered risk of cardiovascular and respiratory diseases.

CHAPTER 2

METHODS

Subjects

This study was conducted with the population of Bornean orangutans housed in the Rainforest exhibit at the Cleveland Metroparks Zoo (listed in Table 1 and pictured in Figures 1 a-d). The orangutan enclosure consists of an indoor space with a large, domed glass ceiling and a large rock structure with artificial tree that allows the animals to access elevated space. This population includes one adult male (Tiram), two adult females (Kayla and Kera Wak), and an adolescent female (Merah, offspring of Tiram and Kera Wak). Tiram and Kayla have both been at the zoo since 1994, and have had three offspring together. Kera joined the group in 2000, and Merah is her first offspring. All animals were housed in accordance with Cleveland Metroparks Zoo animal care and use guidelines.

Table 1 – Subject information

Name	Sex	Age at the beginning of study
Tiram	Male	31 (born 1986)
Kayla	Female	31 (born 1986)
Kera Wak	Female	18 (born 1998)
Merah	Female	2 (born 2014)


Figure 1 (a) – Tiram


Figure 1 (b) – Kayla


Figure 1 (c) – Kera


Figure 1 (d) – Merah

Experimental Phases

This diet manipulation was conducted in three phases: Baseline, Transition, and Post. Each phase was defined by a concurrent diet condition, as detailed below. Phases continued as long as was necessary to collect eight hours of behavioral observation for each subject, and one serum sample from each donating subject. All experimental manipulations were approved by the animal care and use committee at the Cleveland Metroparks Zoo.

Diet Change

Baseline diet

The baseline phase served to establish the normal behavioral patterns on the initial diet, which was the provision of biscuits supplemented with produce. Food items and allotment for this diet are listed in Table 2. Other food items not listed here were used for snacks and enrichment.

Table 2 – Initial diet food items and daily allotment for entire group

Food item	**Grams for entire group**
Mazuri L/S Cinnamon Biscuit	920
Apple	375
Banana	555
Carrot	300
Oranges	585
Sweet potato	625
Greens (romaine)	1440
Total	**4800**

Transitional diet

The goal for the biscuit-free diet was to ultimately decrease starch and increase fiber content by eliminating biscuits and increasing vegetables and leafy greens. To ease the subjects into the new diet, a transition phase was conducted. During this phase, biscuits remained in the diet while the non-biscuit foods were adjusted to the levels planned for the new diet (Table 3). This also provided zoo staff the opportunity to begin optimizing the alternative food items before biscuits were removed in the final stage.

It was important to ensure that enrichment items also reflected these nutritional goals. Keepers were asked to use only unsweetened food items from an approved list (Table 4), and to feed no more than 318 grams of a single enrichment food item per day. This limit of 318 grams ensured that the overall diet did not exceed the desired amount of dietary starch. Due to a higher starch content, some food items had a maximum daily allowance of under 318 grams. In these cases, keepers could supplement with one other item to meet the maximum daily amount. Any snacks, enrichment activities, and rewards for training, were to be included in this measure.

Table 3 - Transitional diet food items and daily allotment for each subject

Food item	**Grams for entire group**	**Tiram**	**Kayla**	**Kera/ Merah**
Mazuri L/S cinnamon biscuit	920	368	184	368
Apple	375	150	75	150
Banana	555	222	111	222
Broccoli	300	120	60	120
Oranges	585	234	117	234
Zucchini	625	250	125	250
Greens (romaine)	3000	1200	600	1200
Total	**6360**	**2544**	**1272**	**2544**

Table 4 – Approved enrichment items and maximum grams permitted per subject, per day

OTHER	
Food item	**Grams permitted**
Applesauce	318
Peanut butter	318
Ketchup	238
Mustard	319

VEGETABLES	
Food item	**Grams permitted**
Brussel sprout	158
Dandelion	119
Romaine	318
Endive	318
Spinach	318
Kale	318
Collard greens	318
Mustard greens	318
Broccoli	238
Green bean	158
Cucumber	318
Zucchini	318
Pumpkin	95
Celery	318
Cauliflower	318

NUTS/SEEDS/LEGUMES		
Food item	**Grams permitted**	**If feeding whole nuts w/shells**
Sunflower seeds	318	158
Peanuts	238	158
Almonds	238	158
Pistachios	318	63
Walnuts	318	238
Filberts	238	210
Brazil nuts	318	316
Pecans	318	423

FRUIT	
Food item	**Grams permitted**
Strawberry	318
Blueberry	238
Mango	318
Papaya	238
Cantaloupe	318
Honeydew	318
Pear	238
Plum	318
Peach	318
Watermelon	318
Tomato	318
Coconut	318

Development of the biscuit-free diet

Upon completion of data collection for the transition phase, the subjects were weaned off biscuits over the course of 10 days (amount given was decreased by 10% increments each day). As soon as weaning was complete, the subjects were eating the proposed final diet (Table 5), and the “Post” experimental phase began.

However, due to subject preferences and arising health concerns, adjustments were made periodically in the transition and final phases (Table 6). One change was the addition of resistant starch to the diets. This type of starch is found in legumes, seeds, and whole grains, but has a low glycemic index, and is fermented by the hind gut and used by the body like fiber (Less et al., 2013). Less (2012) reported that a biscuit-free diet with resistant starch was associated with an increase in triglycerides, but was overall equally effective at improving health parameters as a biscuit-free diet without it. As such, resistant starch was a useful addition when concerns about the subjects' fiber consumption arose.

Table 5 – Proposed biscuit-free diet food items and daily allotment for each subject

Food item	**Tiram (g)**	**Kayla (g)**	**Kera (g)**	**Merah (g)**
Dandelion	2000	1000	1200	800
Apple	60	30	36	24
Banana	60	30	36	24
Carrot	60	30	36	24
Oranges	60	30	36	24
Green beans	80	40	48	32
Romaine	2000	1000	1200	800
Broccoli	80	40	48	32
Zucchini	80	40	48	32
Alfalfa	600	300	360	240
Total	**5080**	**2540**	**3048**	**2032**

Table 6 – Changes made to diet between start of transition and end of experimental period

Date	**Issue addressed**	**Change(s) made**
8/9/2017	Kera and Merah not finishing broccoli/zucchini	- Increased Kera and Merah's green beans
9/22/2017	New goals: - Encourage consumption of greens - Allow as much on-exhibit scatter feeding as possible	- Feed dandelion greens and 25% of vegetables as a morning meal in holding - Scatter-feed remaining 75% of vegetables and 50% of romaine on exhibit throughout the day - Feed other 50% of romaine in the evening - Use fruit only for enrichment

Table 6 continued

10/5/2017	- Subjects rejecting dandelion - Merah losing weight	- Reduce dandelion, compensated with endive - Increase total romaine - Add 100g of biscuits back into Merah's diet (provide throughout the day, when apart from Kera)
10/16/2017	- Kera losing weight	- Eliminate dandelion from Kera and Merah's diet
10/16/2017	- Kera and Merah do not eat dandelion	- Replace with romaine
10/18/217	- Concern of inadequate fiber consumption	- Added resistant starch for all subjects - Added ground flax seed for Kera
10/20/2017	- Kera weight loss - Goal: wean Merah off biscuits without weight loss	- Increased green beans for Kera and Merah - Decreased Merah's biscuits by 10g
10/28/2017	- Fiber consumption - Merah's biscuits	- Increased resistant starch for all subjects - Decreased Merah's biscuits by 10 more grams - Increased Merah's green beans
12/2/2017	- Loose stool for all subjects	- Temporarily removed alfalfa (from 12/2-12/5) to assess fecal consistency without it
12/15/2017	- Kera's loose stool, need for a fiber replacement	- Removed Kera's resistant starch - Added a chia seed mixture to increase protein
12/18/2017	- Kera accepting chia seed mixture	- Increase Kera's chia to twice per day

Table 6 continued

12/21/2017	Goal: increase Kera’s intake	- Increase Kera’s overall diet by 10% - Increase on-exhibit greens for whole group (to ensure Kera’s increase while compensating for competition from others)

Final biscuit-free diet

The biscuit-free diet for each subject, adjusted for subject preferences and health concerns, is listed in Table 7.

Table 7 – Final biscuit-free diet for each subject

Food item	Tiram (g)	Kayla (g)	Food item	Kera (g)	Merah (g)
AM FEEDING					
Romaine	2750	1100	**Romaine**	2200	880
Green beans	231	198	**Green beans**	225	99
			Mazuri L/S cinnamon biscuit		40
Gummy vitamin	1	1	**Gummy vitamin**	1	1
Hi-Maize resistant starch	30	15	**Hi-Maize resistant starch**		10
			Flax seed, ground and mixed with water	66	0
Food item	**Tiram (g)**	**Kayla (g)**	**Food item**	**Kera (g)**	**Merah (g)**
AM FEEDING					
Chia seed mix		14g chia, 30g applesauce, 30g water	**Chia seed mix**	30g chia, 30g applesauce, 60g water	5g chia, 10g applesauce, 20g water
On-exhibit morning feeding					
Grass hay	1650				
Dandelion	1760				
Endive	1650				
FRUITS – to be fed only during training or in a challenging fashion					
Banana	66	33	**Banana**	60	26
Oranges	66	33	**Oranges**	60	26

Table 7 continued

Apple	66	33	**Apple**	60	26
VEGETABLES – to be scatter fed on exhibit					
Carrot	90	45	**Carrot**	80	35
Broccoli	90	45			
Zucchini	90	45			
MID-DAY SHIFT – fed on exhibit					
Dandelion		1760	**Endive**		1650
PM FEEDING					
Romaine	990	660	**Romaine**	1430	660
			Mazuri L/S cinnamon biscuit		40
			Cucumber	80	35
			Celery	80	35
Chia seed mix		14g chia, 30g applesauce, 30g water	**Chia seed mix**	30g chia, 30g applesauce, 60g water	
Centrum vitamin	1	1	**Centrum vitamin**	1	
Evening on-exhibit scatter feeding					
Romaine	3190				

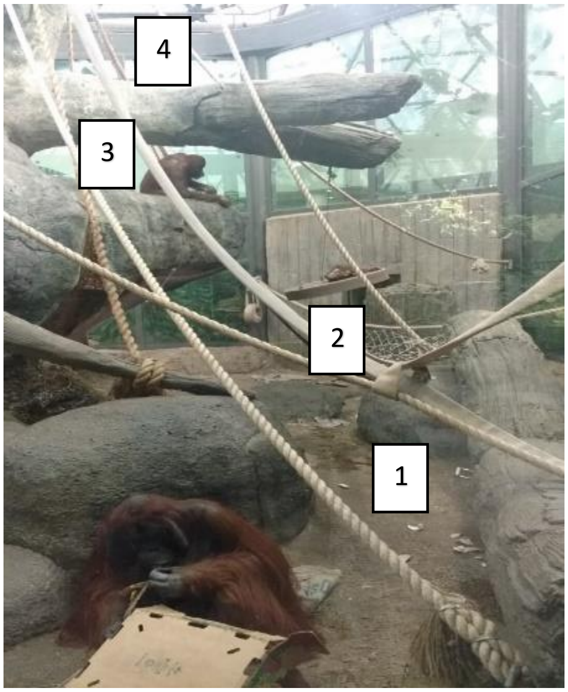
Behavioral Data Collection

On observation days, regular zoo hours were divided into three “time periods”: Morning (1000-1200), Mid-day (1200-1500), and Evening (1500-1700). The Mid-day period was one hour longer than the others to accommodate daily “shifts”, where the animals were removed from the exhibit for a short period of time to allow for exhibit maintenance.

During each observation period, subjects were observed for a 10-minute focal follow (“observation session”) using the ethogram listed in Table 8. Each phase consisted of 16 sessions per subject, per time period. Because each session was 10 minutes long and there were 3 time periods, this amounted to 8 hours of observation for each subject, per phase (or 96 total observation hours for the complete study).

Undesirable behaviors were collected by scans and "all occurrence" tracking, allowing them to be quantified by the number of times they occurred during the session. Food processing and locomotive behaviors were tracked "continuously", or quantified by the percentage of time during the session that the subject spent engaging in them. On every 30 second interval, the subject's location and current behavior was recorded. There were four possible locations: (1) "Ground floor", or the lowest level of the exhibit, (2) "Ropes or hammock", or any structure suspended below the second level, (3) "Second level", which included any areas that require climbing to access but are still lower than the tree, and (4) "Tree", or the artificial tree that encompasses the highest area of the exhibit (see Figure 2).

Figure 2 – Photo of orangutan exhibit at the Cleveland Metroparks Zoo with labeled locations



Baseline phase

The baseline phase took place from June 1 – July 20, with an exception for the use of three earlier-recorded videos: one of Tiram from the evening of Apr. 14, one of Kayla from the evening of Apr. 14, and one of Merah from the morning of May 19. Observations for this phase were collected via video recording to allow observations to begin despite further editing of the ethogram. Upon the ethogram's completion, videos were scored using the ZooMonitor application (Ross et al., 2016). All observations during the later phases were taken live using ZooMonitor. Reliability testing was done to ensure that videos were at least 90% accurate to live observations.

Transition phase

The transition phase took place from August 7 – September 11. It should be noted that, during this phase, Tiram chose to stay off exhibit after the mid-day shift from August 27 – August 31. As such, no evening data were collected for him on these days. Collection continued as normal for the other subjects.

Post phase

The biscuit-free diet and, thus, the final phase, took place from October 2 – December 22. During this phase, Kera experienced some gastrointestinal distress, as evidence by extremely loose stool for an extended period of time. As such, she and Merah were kept off exhibit to be monitored on December 17, so no data were collected for them on this day. Collection continued as normal for the other subjects. A volunteer collected one day of observational data during this phase. Reliability testing was conducted to ensure at least 90% inter-observer reliability.

Table 8 – Ethogram of selected behaviors

Continuous behaviors		
Behavior	**Modifier**	**Description**
Food processing	Consuming	Act of moving food to mouth/chewing/swallowing
	Foraging	Any food-related behavior besides consumption (ex. digging through hay)
Locomotion	Terrestrial	Moving at least one body length across the same level of ground
	Climbing	Moving up or down between levels of enclosure (includes locomoting using ropes)
	Other	Any locomotive behavior not otherwise specified here (Ex. swinging, rolling in hay)

Location channels (record on each interval)	
Location	**Description**
Ground floor	Concrete floor or on rocks/logs one step above
Ropes or hammock	Hanging from/sitting on hammock or ropes below second level
Second level	Tall log, upper rock, or ropes above rock but below tree (Areas that required climbing to access, but still lower than tree)
Tree	Highest area of enclosure (on ropes among tree or in branches)
Out of view	Animal out of sight

Interval behaviors		
Behavior	**Modifier**	**Description**
Undesirable	R/R	Regurgitating in mouth, into hand, or onto floor, and reingesting
	Coprophagy	Ingesting feces
	Urine drinking	Urinating onto ground/into hand followed by ingesting
	Hair plucking	Pulling hairs out of skin (on self or another individual)
	Other	Any undesirable behavior not otherwise specified here
Social	Neutral	Non-aggressive interaction with another animal
	Mother/daughter	Interactions between Kera and Merah
	Aggression towards conspecific	Any act of aggression toward another animal
	Neutral towards guests	Any non-aggressive interaction with guests
	Aggression toward guests	Charging/hitting/biting at glass in response to guests
	Sticking out tongue	Opening mouth to show tongue
	Other social	Any social behavior not otherwise specified here

Attention		Animal pays attention to (but doesn’t interact with) someone/something outside the exhibit for at least 3 sec.
Manipulating object		Interaction with enrichment object in enclosure when not food searching
Self-directed	Scratching	Self-scratching
	Skin picking	Animal separates hair and picks at skin without removing hair
	Nose picking	Picking at nostrils or blowing nose
	Teeth picking	Use of finger/other object to pick teeth
	Other	Any other self-directed behavior
Yawning		Mouth opening widely to bare teeth/sharply inhale
Nursing		Breastfeeding (Kera or Merah)
Elimination		Urination or defecation
Chewing		Focal animal is constantly chewing without having put new food in mouth since the previous interval
Inactive		Still and performing no other behavior
Behavior not visible		Animal in view, but behavior not distinguishable
Out of view		Animal out of sight

Behavioral Data Analysis

Food consumption, foraging, and locomotion behaviors were tracked continuously, and analyzed in terms of the percent of observation time that was spent engaging in the behavior (ZooMonitor tracked the number of seconds, and those values were divided by the total number of seconds in the observation session for analysis). The focal subject's location was recorded at every 30-second interval, and these data were analyzed in terms of the percent of intervals at each location. The same interval-based methods were used for the behaviors listed in Table 8.

Parametric one-way ANOVAs were used to evaluate changes in behaviors across conditions (baseline, transition, and post) for each subject. Least significant difference post-hoc tests were used to further determine which behaviors/conditions showed changes. Alpha was set at 0.05 for all statistical tests.

Health data Collection

Serum samples were collected from the two subjects who were trained for unrestrained, awake venipuncture, Tiram and Kayla. Tiram provided one sample per phase. Kayla provided one sample during the baseline and post phases, but not during the transition.

Health Data Analysis

Blood samples were analyzed by enzyme immunoassay in the Raghanti laboratory at Kent State University using commercially available ELISA kits for leptin (Mercodia 10-1199-01) and insulin (Mercodia 10-1132-01). Glucose, triglycerides, and total cholesterol were measured using an IDEXX vettest autoanalyzer at the Cleveland Metroparks Zoo Endocrinology laboratory. All measures were previously validated for use with orangutan serum.

CHAPTER 3

RESULTS

Continuous Behaviors

All phase means for each subject are listed in Tables 9 a-c, with all significant post-hoc values graphed in Figures 3 a-f. A (+) or (-) to the right of the LSD post hoc significance level indicates whether the change between phases was an increase or a decrease in that behavior for the second phase mentioned.

Food consumption

Kera and Merah had significant changes in consumption behavior (see Table 9a). Shown in Figure 3a, Kera's significant change was an increase in consumption behaviors in the morning of the transition phase relative to both base and post. Merah showed an increase in consumption behavior during the post phase relative to both base and transition (Figure 3b).

Table 9(a) Percent of time spent in food consumption

SUBJECT	AM	MID	PM
Kayla	Base = 22.552 ± 9.017 Transition = 43.719 ± 10.312 Post = 46.875 ± 11.284 $F_{2,47}$ = 1.666, p = 0.200	Base = 18.906 ± 6.620 Transition = 27.875 ± 8.333 Post = 29.792 ± 8.497 $F_{2,47}$ = 0.546, p = 0.583	Base = 37.219 ± 9.800 Transition = 18.385 ± 8.207 Post = 33.500 ± 9.609 $F_{2,47}$ = 1.167, p = 0.320
Tiram	Base = 16.406 ± 8.245 Transition = 24.344 ± 8.203 Post = 35.760 ± 9.776 $F_{2,47}$ = 1.230, p = 0.302	Base = 18.906 ± 8.219 Transition = 22.458 ± 8.495 Post = 13.021 ± 7.928 $F_{2,47}$ = 0.336, p = 0.716	Base = 15.833 ± 7.591 Transition = 8.524 ± 5.908 Post = 27.198 ± 9.600 $F_{2,45}$ = 1.361, p = 0.267

Table 9(a) continued

Kera	Base = 13.531 ± 6.347 Transition = 37.740 ± 9.939 Post = 10.063 ± 4.887 $F_{2,47}$ = 4.185, p = 0.022 **LSD base-trans = 0.025 (+)** **LSD trans-post = 0.011 (-)**	Base = 29.969 ± 8.657 Transition = 17.083 ± 5.413 Post = 22.510 ± 8.873 $F_{2,47}$ = 0.686, p = 0.509	Base = 18.813 ± 8.583 Transition = 8.000 ± 2.847 Post = 7.890 ± 3.414 $F_{2,46}$ = 1.242, p = 0.299
Merah	Base = 2.781 ± 1.245 Transition = 13.539 ± 3.886 Post = 18.156 ± 7.473 $F_{2,48}$ = 2.567, p = 0.088 **LSD base-post = 0.032 (+)**	Base = 6.135 ± 3.678 Transition = 11.822 ± 4.997 Post = 22.344 ± 4.885 $F_{2,46}$ = 3.345, p = 0.044 **LSD base-post = 0.014 (+)**	Base = 2.521 ± 1.253 Transition = 6.281 ± 1.723 Post = 15.422 ± 4.215 $F_{2,46}$ = 6.178, p = 0.004 **LSD base-post = 0.001 (+)** **LSD trans-post = 0.019 (+)**

Figure 3(a) Significant changes in Kera's consumption

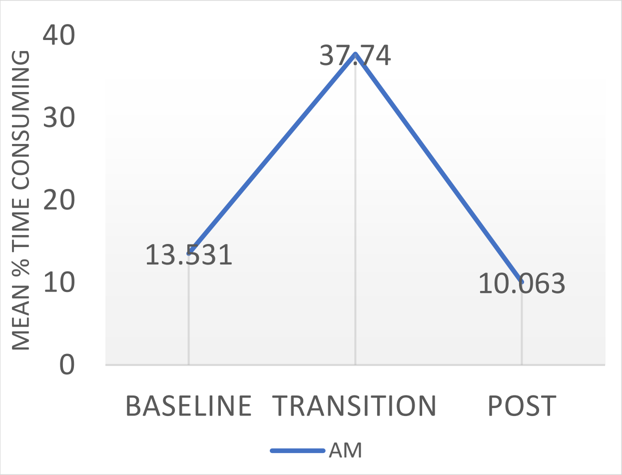
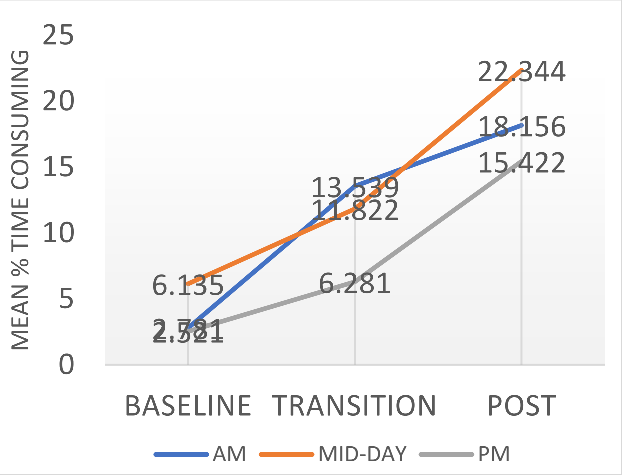


Figure 3(b) Significant changes in Merah's consumption



Foraging

Only Merah showed a significant change in foraging behavior, with an increase in foraging occurring mid-day during the transition period relative to base and post (see Table 9b and Figure 3c).

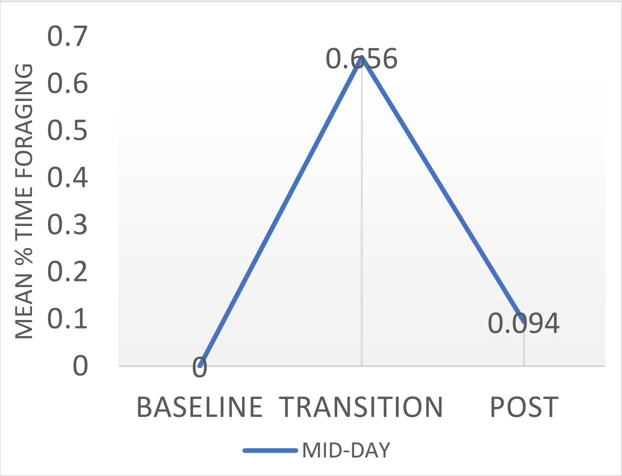
Table 9(b) Percent of time spent foraging

SUBJECT	**AM**	**MID**	**PM**
Kayla	Base = 0.917 ± 0.793 Transition = 1.552 ± 0.739 Post = 1.646 ± 1.214 $F_{2,47}$ = 0.178, p = 0.837	Base = 2.125 ± 1.164 Transition = 5.563 ± 2.803 Post = 1.478 ± 0.726 $F_{2,47}$ = 1.504, p = 0.233	Base = 5.240 ± 2.229 Transition = 2.354 ± 1.732 Post = 2.969 ± 2.676 $F_{2,47}$ = 0.458, p = 0.635

Table 9(b) continued

Tiram	Base = 0.833 ± 0.569 Transition = 0.958 ± 0.357 Post = 0.271 ± 0.185 $F_{2,47}$ = 0.828, p = 0.444	Base = 0.708 ± 0.488 Transition = 2.031 ± 1.345 Post = 1.760 ± 1.173 $F_{2,47}$ = 0.428, p = 0.654	Base = 0.000 ± 0.000 Transition = 1.524 ± 1.486 Post = 0.000 ± 0.000 $F_{2,45}$ = 1.210, p = 0.308
Kera	Base = 1.365 ± 1.218 Transition = 0.906 ± 0.535 Post = 1.042 ± 0.603 $F_{2,47}$ = 0.078, p = 0.925	Base = 0.510 ± 0.510 Transition = 1.406 ± 0.609 Post = 1.063 ± 0.889 $F_{2,47}$ = 0.431, p = 0.653	Base = 0.469 ± 0.469 Transition = 0.667 ± 0.201 Post = 1.378 ± 1.366 $F_{2,46}$ = 0.340, p = 0.714
Merah	Base = 0.823 ± 0.657 Transition = 0.539 ± 0.295 Post = 1.438 ± 0.787 $F_{2,48}$ = 0.575, p = 0.566	Base = 0.000 ± 0.000 Transition = 0.656 ± 0.333 Post = 0.094 ± 0.075 $F_{2,46}$ = 3.450, p = 0.041 **LSD base-trans = 0.019 (+)** **LSD trans-post = 0.042 (-)**	Base = 0.115 ± 0.104 Transition = 1.385 ± 0.593 Post = 0.944 ± 0.581 $F_{2,46}$ = 1.857, p = 0.168

Figure 3(c) Significant changes in Merah's foraging



Locomotion

Kayla, Tiram, and Merah all showed significant increases in locomotion (see Table 9c). Kayla's increase occurred in the mid-day period of the post phase relative to the transition phase (Figure 3d). Tiram's locomotion increased in the morning and evening of the post phase (Figure 3e) Merah's locomotion increased during the mid-day of the transition phase relative to baseline (Figure 3f).

Table 9(c) Percent of time spent locomoting

SUBJECT	AM	MID	PM
Kayla	Base = 1.229 ± 0.675 Transition = 2.167 ± 1.024 Post = 1.729 ± 0.652 $F_{2,47}$ = 0.324, p = 0.712	Base = 4.979 ± 1.230 Transition = 4.365 ± 1.076 Post = 7.948 ± 1.303 $F_{2,47}$ = 2.521, p = 0.092 **LSD trans-post = 0.041 (+)**	Base = 4.552 ± 1.276 Transition = 6.438 ± 3.661 Post = 9.208 ± 2.264 $F_{2,47}$ = 0.817, p = 0.448
Tiram	Base = 1.052 ± 0.600 Transition = 2.031 ± 0.802 Post = 5.031 ± 2.104 $F_{2,47}$ = 2.376, p = 0.105 **LSD base-post = 0.042 (+)**	Base = 3.573 ± 1.451 Transition = 4.510 ± 1.514 Post = 3.198 ± 1.121 $F_{2,47}$ = 0.242, p = 0.786	Base = 6.146 ± 1.628 Transition = 2.179 ± 0.792 Post = 6.958 ± 1.657 $F_{2,45}$ = 2.923, p = 0.065 **LSD trans-post = 0.028 (+)**
Kera	Base = 2.438 ± 0.646 Transition = 2.250 ± 0.796 Post = 2.219 ± 0.991 $F_{2,47}$ = 0.021, p = 0.980	Base = 3.260 ± 0.866 Transition = 4.313 ± 1.284 Post = 4.240 ± 1.257 $F_{2,47}$ = 0.260, p = 0.772	Base = 2.677 ± 0.936 Transition = 3.844 ± 1.465 Post = 2.344 ± 0.678 $F_{2,46}$ = 0.521, p = 0.598
Merah	Base = 9.750 ± 2.809 Transition = 13.157 ± 2.249 Post = 12.875 ± 2.255 $F_{2,48}$ = 0.594, p = 0.556	Base = 9.646 ± 1.701 Transition = 19.111 ± 3.910 Post = 12.146 ± 2.858 $F_{2,46}$ = 2.773, p = 0.073 **LSD base-trans = 0.027 (+)**	Base = 13.375 ± 2.503 Transition = 17.354 ± 3.497 Post = 15.100 ± 2.112 $F_{2,46}$ = 0.521, p = 0.597

Figure 3(d) Significant changes in Kayla's locomotion

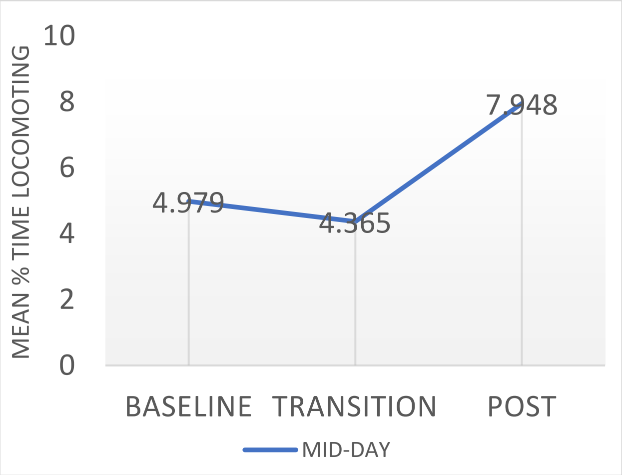


Figure 3(e) Significant changes in Tiram's locomotion

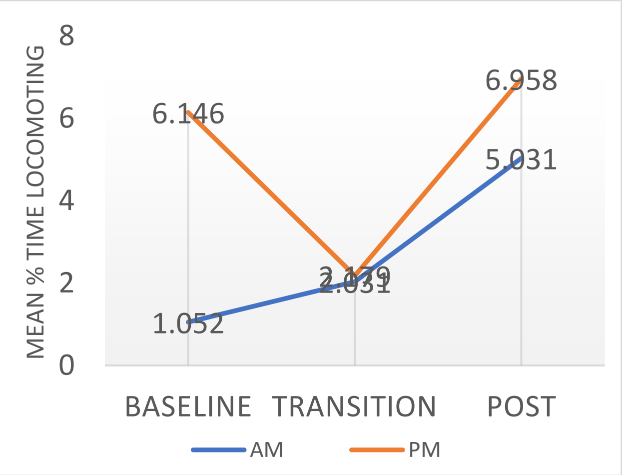
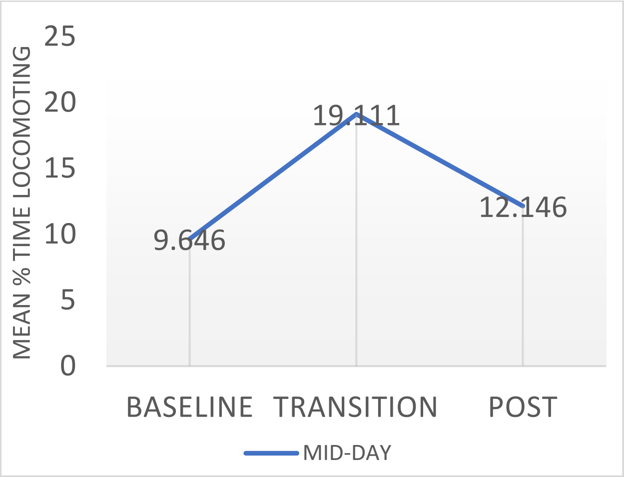


Figure 3(f) Significant changes in Merah's locomotion



Space Use

Observation sessions were 10 minutes long and the focal subject's location and behavior were recorded at every 30-second interval. For each observation session, the percent of visible intervals spent at each level of the enclosure was calculated. All phase means for each subject are listed in Tables 10 a-d, with all significant post-hoc values graphed in Figures 4 a-k.

Use of Ground Level

Kayla, Tiram, and Kera all showed significant changes in their percent of intervals recorded on the ground (see Table 10a). For Kayla, ground use decreased during mid-day of the transition phase relative to baseline and then increased again during mid-day of the post phase, and decreased in the evening for the post phase relative to both baseline and transition (Figure 4a). Tiram's time on the ground increased significantly in the evening for the transition and post phases (Figure 4b). Kera spent more time on the ground during the mid-day of the post phase (Figure 4c).

Table 10(a) Percent of intervals on the ground

SUBJECT	**AM**	**MID**	**PM**
Kayla	Base = 84.757 ± 8.617 Transition = 88.438 ± 6.918 Post = 98.750 ± 1.250 $F_{2,47}$ = 1.276, p = 0.289	Base = 90.833 ± 6.319 Transition = 59.326 ± 11.412 Post = 92.006 ± 3.926 $F_{2,47}$ = 5.556, p = 0.007 **LSD base-trans = 0.007 (-)** **LSD trans-post = 0.005 (+)**	Base = 97.188 ± 2.813 Transition = 99.375 ± 0.625 Post = 84.691 ± 6.933 $F_{2,47}$ = 3.340, p = 0.044 **LSD base-post = 0.047 (-)** **LSD trans-post = 0.021 (-)**
Tiram	Base = 95.938 ± 4.063 Transition = 96.563 ± 3.438 Post = 93.750 ± 6.250 $F_{2,47}$ = 0.097, p = 0.908	Base = 99.688 ± 0.313 Transition = 93.438 ± 5.138 Post = 100.000 ± 0.000 $F_{2,47}$ = 1.552, p = 0.223	Base = 95.045 ± 2.270 Transition = 100.000 ± 0.000 Post = 99.671 ± 0.329 $F_{2,45}$ = 4.075, p = 0.024 **LSD base-trans = 0.016 (+)** **LSD base-post = 0.020 (+)**
Kera	Base = 1.266 ± 0.973 Transition = 1.667 ± 1.667 Post = 11.354 ± 7.161 $F_{2,47}$ = 1.780, p = 0.180	Base = 11.957 ± 6.422 Transition = 6.415 ± 2.604 Post = 39.583 ± 12.255 $F_{2,47}$ = 4.778, p = 0.013 **LSD base-post = 0.020 (+)** **LSD trans-post = 0.006 (+)**	Base = 6.944 ± 6.242 Transition = 21.563 ± 9.882 Post = 14.000 ± 9.026 $F_{2,46}$ = 0.754, p = 0.476
Merah	Base = 21.581 ± 9.497 Transition = 27.106 ± 6.954 Post = 28.125 ± 8.932 $F_{2,48}$ = 0.170, p = 0.844	Base = 15.951 ± 7.354 Transition = 26.953 ± 7.557 Post = 41.108 ± 11.185 $F_{2,46}$ = 2.035, p = 0.143	Base = 41.581 ± 8.877 Transition = 27.900 ± 7.879 Post = 23.782 ± 8.982 $F_{2,46}$ = 1.181, p = 0.317

Figure 4(a) Significant changes in Kayla's ground use

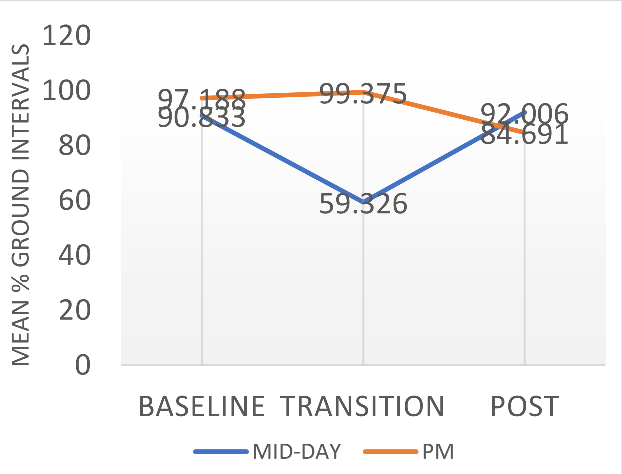


Figure 4(b) Significant changes in Tiram's ground use

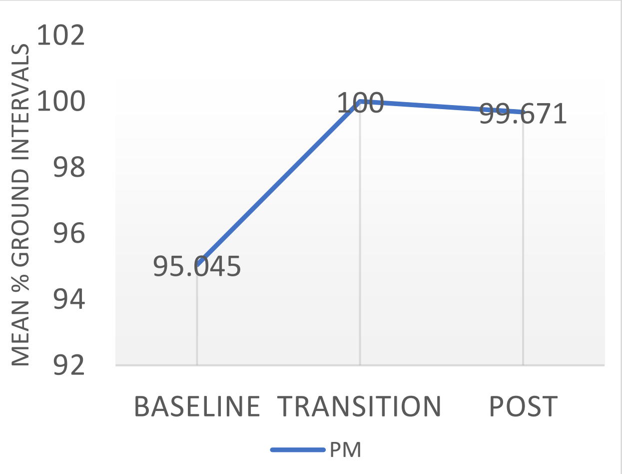
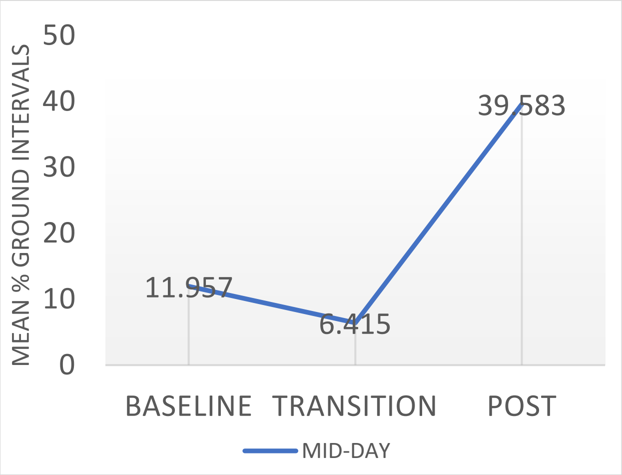


Figure 4(c) Significant changes in Kera's ground use



Use of Ropes/hammock

Kayla, Kera, and Merah showed significant changes in their use of the ropes and hammock (see Table 10b). Kayla spent more time on the ropes/hammock during the evenings of the post phase relative to baseline (Figure 4d). Kera decreased time spent on ropes/hammock during the morning of the transition phase relative to baseline, and in the afternoon of the post phase relative to transition (Figure 4e). Merah decreased the amount of time spent on ropes/hammock during the mid-day and evening of the post phase relative to baseline and transition, respectively (Figure 4f).

Table 10(b) Percent of intervals on the ropes/hammock

SUBJECT	**AM**	**MID**	**PM**
Kayla	Base = 0.660 ± 0.451 Transition = 0.313 ± 0.313 Post = 0.313 ± 0.313 $F_{2,47}$ = 0.643, p = 0.741	Base = 0.625 ± 0.427 Transition = 0.954 ± 0.513 Post = 0.313 ± 0.313 $F_{2,47}$ = 0.568, p = 0.570	Base = 0.000 ± 0.000 Transition = 0.625 ± 0.625 Post = 1.634 ± 0.628 $F_{2,47}$ = 2.599, p = 0.085 **LSD base-post = 0.029 (+)**
Tiram	Base = 0.000 ± 0.000 Transition = 0.313 ± 0.313 Post = 0.000 ± 0.000 $F_{2,47}$ = 1.000, p = 0.376	Base = 0.000 ± 0.000 Transition = 0.313 ± 0.313 Post = 0.000 ± 0.000 $F_{2,47}$ = 1.000, p = 0.376	Base = 0.938 ± 0.680 Transition = 0.000 ± 0.000 Post = 0.000 ± 0.000 $F_{2,45}$ = 1.777, p = 0.181

Table 10(b) continued

SUBJECT	AM	MID	PM
Kera	Base = 19.655 ± 9.186 Transition = 0.417 ± 0.417 Post = 5.938 ± 4.984 $F_{2,47}$ = 2.691, p = 0.079 **LSD base-trans = 0.029 (-)**	Base = 8.602 ± 3.798 Transition = 16.291 ± 7.058 Post = 0.694 ± 0.694 $F_{2,47}$ = 2.819, p = 0.070 **LSD trans-post = 0.022 (-)**	Base = 1.389 ± 1.389 Transition = 10.938 ± 5.760 Post = 7.000 ± 3.478 $F_{2,46}$ = 1.478, p = 0.239
Merah	Base = 29.518 ± 7.723 Transition = 29.431 ± 6.837 Post = 26.398 ± 5.888 $F_{2,48}$ = 0.066, p = 0.936	Base = 38.159 ± 7.999 Transition = 22.298 ± 6.496 Post = 12.866 ± 5.593 $F_{2,46}$ = 3.622, p = 0.035 **LSD base-post = 0.011 (-)**	Base = 30.996 ± 7.077 Transition = 36.627 ± 7.088 Post = 16.338 ± 4.299 $F_{2,46}$ = 2.653, p = 0.082 **LSD trans-post = 0.030 (-)**

Figure 4(d) Significant changes in Kayla's R/H use

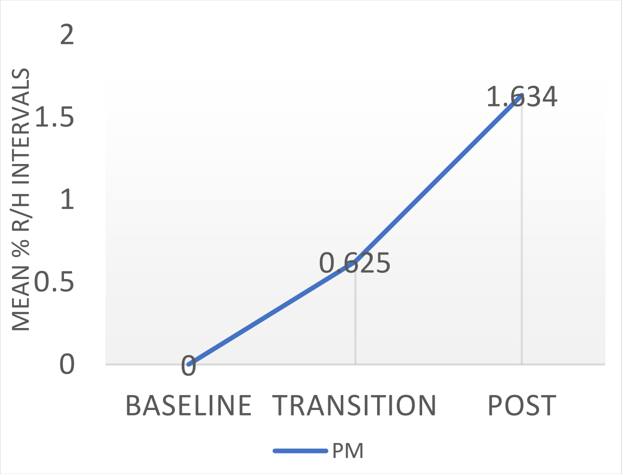


Figure 4(e) Significant changes in Kera's R/H use

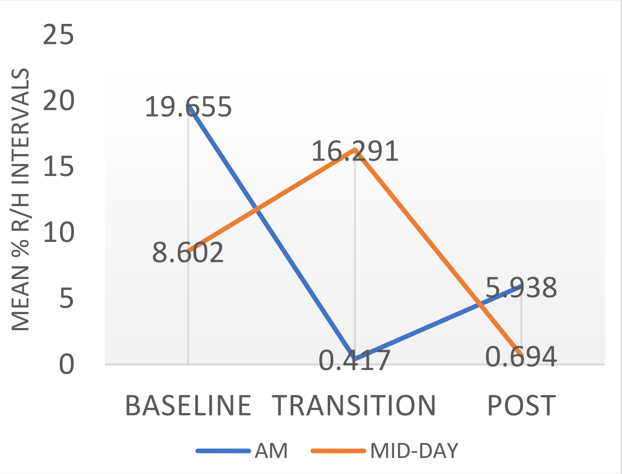
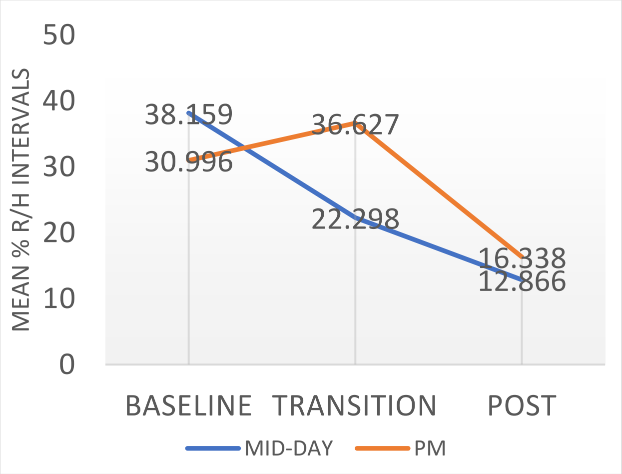


Figure 4(f) Significant changes in Merah's R/H use



Use of Second level

Analysis revealed significant changes in percent of intervals on the second level for Kayla, Tiram, and Kera (see Table 10c). Kayla spent more time on the second level during mid-day the transition phase relative to baseline and post, and during the evening of the post phase relative to transition (Figure 4g). Both Tiram and Kera decreased time spent on the second level in the evening throughout the phases (Figures 4h and 4i).

Table 10(c) Percent of intervals on the second level

SUBJECT	AM	MID	PM
Kayla	Base = 14.583 ± 8.590 Transition = 11.250 ± 6.824 Post = 0.000 ± 0.000 $F_{2,47}$ = 1.456, p = 0.244	Base = 8.542 ± 6.295 Transition = 35.345 ± 11.592 Post = 7.682 ± 3.901 $F_{2,47}$ = 3.923, p = 0.027 **LSD base-trans = 0.021 (+)** **LSD trans-post = 0.018 (-)**	Base = 2.813 ± 2.813 Transition = 0.000 ± 0.000 Post = 13.362 ± 6.823 $F_{2,47}$ = 2.733, p = 0.076 **LSD trans-post = 0.032 (+)**
Tiram	Base = 4.063 ± 4.063 Transition = 3.125 ± 3.125 Post = 6.250 ± 6.250 $F_{2,47}$ = 0.118, p = 0.889	Base = 0.313 ± 0.313 Transition = 6.250 ± 5.072 Post = 0.000 ± 0.000 $F_{2,47}$ = 1.441, p = 0.247	Base = 4.018 ± 1.932 Transition = 0.000 ± 0.000 Post = 0.329 ± 0.329 $F_{2,45}$ = 3.612, p = 0.035 **LSD base-trans = 0.022 (-)** **LSD base-post = 0.029 (-)**
Kera	Base = 79.079 ± 9.794 Transition = 90.417 ± 6.885 Post = 66.667 ± 11.463 $F_{2,47}$ = 1.541, p = 0.225	Base = 79.441 ± 8.533 Transition = 75.280 ± 8.490 Post = 52.321 ± 11.688 $F_{2,47}$ = 2.273, p = 0.115	Base = 91.667 ± 6.455 Transition = 67.188 ± 10.438 Post = 36.000 ± 11.641 $F_{2,46}$ = 8.191, p = 0.001 **LSD base-post = 0.000 (-)** **LSD trans-post = 0.029 (-)**
Merah	Base = 43.292 ± 9.416 Transition = 42.928 ± 10.805 Post = 36.415 ± 9.715 $F_{2,48}$ = 0.147, p = 0.864	Base = 44.015 ± 9.237 Transition = 42.709 ± 8.495 Post = 45.546 ± 11.265 $F_{2,46}$ = 0.021, p = 0.979	Base = 24.924 ± 8.179 Transition = 35.161 ± 9.040 Post = 28.148 ± 9.325 $F_{2,46}$ = 0.357, p = 0.702

Figure 4(g) Significant changes in Kayla's 2nd level use

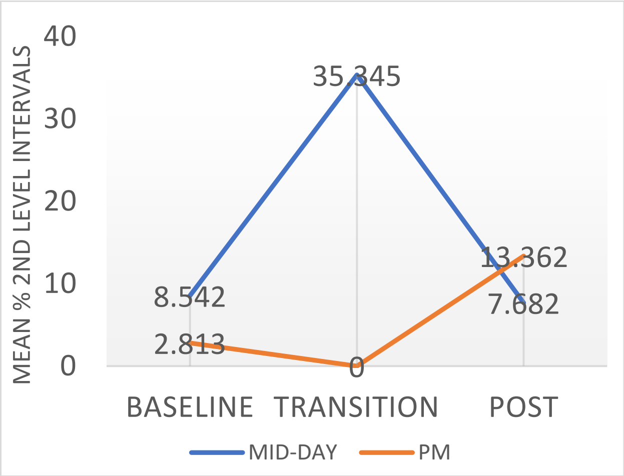


Figure 4(h) Significant changes in Tiram's 2nd level use

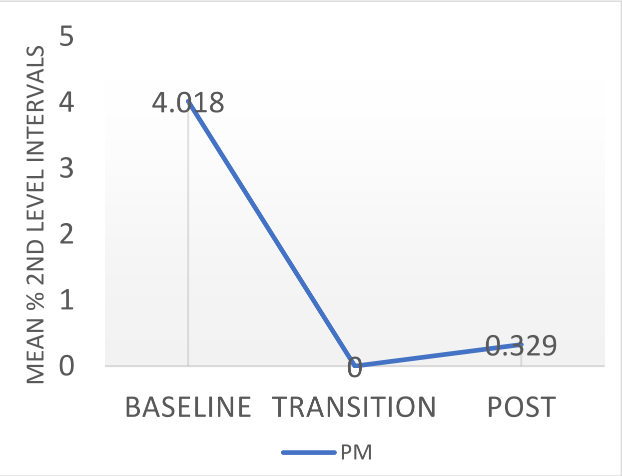
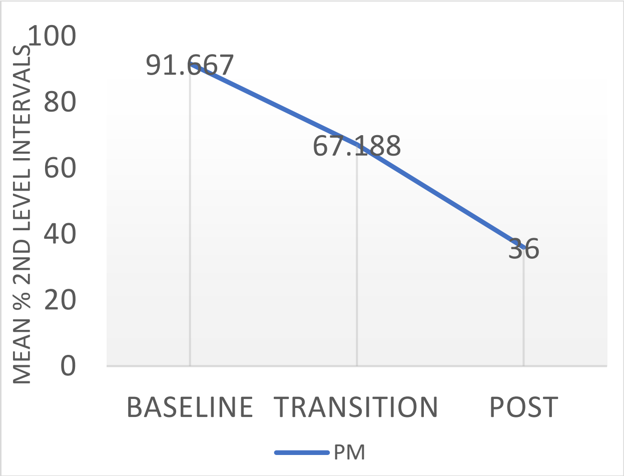


Figure 4(i) Significant changes in Kera's 2nd level use



Use of Tree

As Tiram did not use the tree at any point, measures of this condition are omitted from his results. Kera and Merah both showed significant increases in their time spent in the tree (see Table 10d). Kera spent increasingly more time in the tree in the morning and evening (Figure 4j). Merah's time in the tree increased significantly in the evening, with the greatest percentage of time in the tree in the post phase (Figure 4k).

Table 10(d) Percent of intervals in the tree

SUBJECT	AM	MID	PM
Kayla	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 0.938 ± 0.938 $F_{2,47}$ = 1.000, p = 0.376	Base = 0.000 ± 0.000 Transition = 4.375 ± 3.287 Post = 0.000 ± 0.000 $F_{2,47}$ = 1.771, p = 0.182	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 0.313 ± 0.313 $F_{2,47}$ = 1.000, p = 0.376
Kera	Base = 0.000 ± 0.000 Transition = 1.250 ± 1.250 Post = 16.042 ± 8.538 $F_{2,47}$ = 3.208, p = 0.050 **LSD base-post = 0.028 (+)** **LSD trans-post = 0.041 (+)**	Base = 0.000 ± 0.000 Transition = 2.014 ± 1.485 Post = 7.401 ± 5.126 $F_{2,47}$ = 1.543, p = 0.225	Base = 0.000 ± 0.000 Transition = 0.313 ± 0.313 Post = 43.000 ± 12.486 $F_{2,46}$ = 12.588, p = 0.000 **LSD base-post = 0.000 (+)** **LSD trans-post = 0.000 (+)**
Merah	Base = 5.609 ± 2.547 Transition = 0.535 ± 0.535 Post = 9.063 ± 6.555 $F_{2,48}$ = 1.172, p = 0.319	Base = 1.875 ± 1.360 Transition = 8.039 ± 5.569 Post = 0.481 ± 0.481 $F_{2,46}$ = 1.557, p = 0.222	Base = 2.500 ± 2.500 Transition = 0.313 ± 0.313 Post = 31.732 ± 10.158 $F_{2,46}$ = 8.946, p = 0.001 **LSD base-post = 0.001 (+)** **LSD trans-post = 0.000 (+)**

Figure 4(j) Significant changes in Kera's tree use

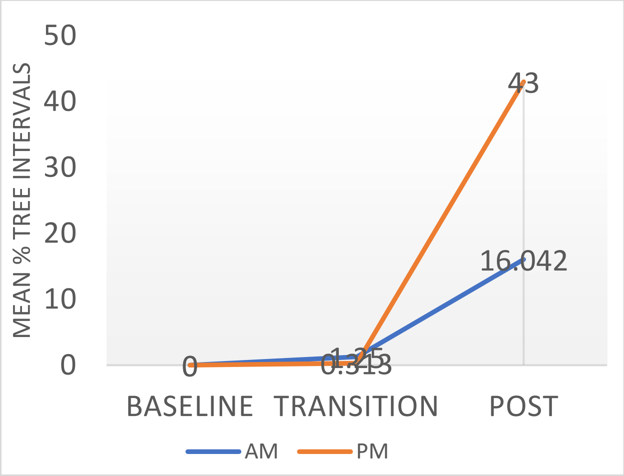
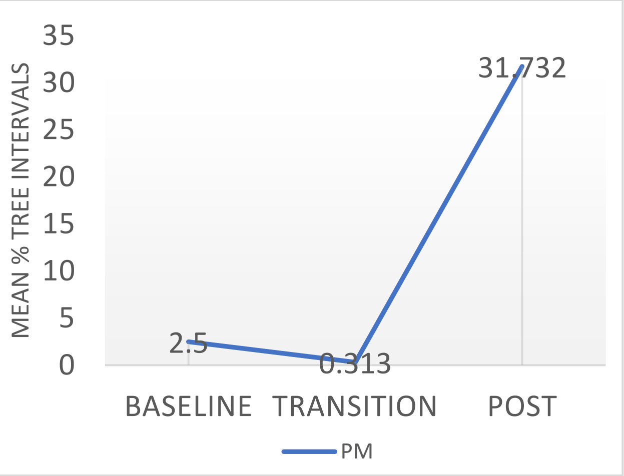


Figure 4(k) Significant changes in Merah's tree use



Interval Behaviors

All behaviors outlined in the ethogram were potential responses to each interval recording. The percent of visible intervals that were scored as each behavior was calculated, and these data were used to track the frequency of each behavior across the study. All phase means for each subject are listed in Tables 11a-h, with all significant post-hoc values graphed in Figures 5a-l.

Food process

Kera and Merah were the only subjects who had significant changes in their continuous feeding behaviors. As shown in Table 11a, they were also the only subjects to show an increase in their interval feeding behaviors. As shown in Figure 5a, Kera had a significant decrease in food processing behavior in the morning, specifically between the transition and post phases. Merah's food processing increased in both the morning and evening (Figure 5b).

Table 11(a) Percent of intervals food processing

SUBJECT	AM	MID	PM
Kayla	Base = 24.653 ± 9.321 Transition = 45.411 ± 10.202 Post = 48.372 ± 11.286 $F_{2,47}$ = 1.574, p = 0.218	Base = 25.418 ± 8.089 Transition = 36.997 ± 10.763 Post = 34.382 ± 9.822 $F_{2,47}$ = 0.398, p = 0.674	Base = 47.900 ± 10.949 Transition = 22.533 ± 9.056 Post = 39.108 ± 9.839 $F_{2,47}$ = 1.666, p = 0.200
Tiram	Base = 20.234 ± 8.711 Transition = 27.352 ± 8.448 Post = 35.099 ± 9.840 $F_{2,47}$ = 0.679, p = 0.512	Base = 23.015 ± 8.755 Transition = 26.168 ± 10.068 Post = 15.313 ± 8.171 $F_{2,47}$ = 0.382, p = 0.685	Base = 17.151 ± 7.720 Transition = 11.071 ± 6.977 Post = 27.620 ± 10.027 $F_{2,45}$ = 0.965, p = 0.389
Kera	Base = 23.544 ± 9.181 Transition = 43.678 ± 11.238 Post = 10.858 ± 5.245 $F_{2,47}$ = 3.452, p = 0.040 **LSD trans-post = 0.012 (-)**	Base = 34.507 ± 9.692 Transition = 21.876 ± 6.180 Post = 22.065 ± 9.006 $F_{2,47}$ = 0.737, p = 0.484	Base = 20.504 ± 8.558 Transition = 10.449 ± 3.209 Post = 9.000 ± 3.754 $F_{2,46}$ = 1.183, p = 0.316
Merah	Base = 4.755 ± 1.741 Transition = 22.408 ± 5.786 Post = 22.259 ± 7.571 $F_{2,48}$ = 3.247, p = 0.048 **LSD base-trans = 0.030 (+)** **LSD base-post = 0.034 (+)**	Base = 9.488 ± 4.403 Transition = 15.826 ± 6.495 Post = 23.621 ± 4.778 $F_{2,46}$ = 1.857, p = 0.168	Base = 4.674 ± 1.697 Transition = 15.024 ± 3.778 Post = 17.519 ± 4.502 $F_{2,46}$ = 3.847, p = 0.029 **LSD base-trans = 0.039 (+)** **LSD base-post = 0.013 (+)**

Figure 5(a) Significant changes in Kera’s food process

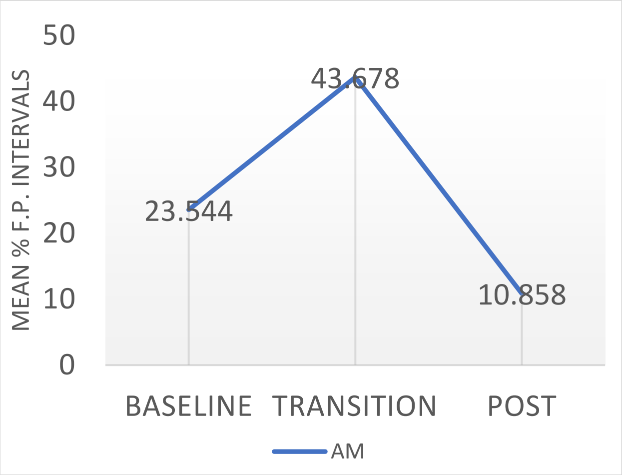
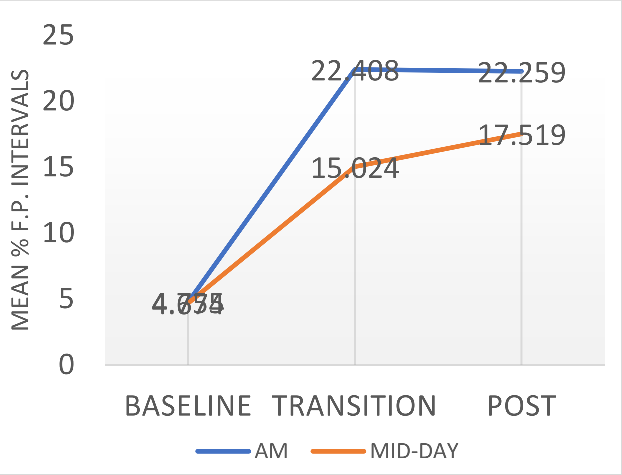


Figure 5(b) Significant changes in Merah’s food process



Locomotion

Tiram and Kera had significant changes in locomotion (see Table 11b). Tiram’s locomotion increased in the morning for the post phase and decreased in the evening of the transition phase (Figure 5c). Kera’s locomotion decreased in the morning of the transition phase (Figure 5d).

Table 11(b) Percent of intervals locomoting

SUBJECT	AM	MID	PM
Kayla	Base = 1.510 ± 0.913 Transition = 2.500 ± 1.369 Post = 1.891 ± 0.779 $F_{2,47}$ = 0.226, p = 0.799	Base = 7.399 ± 2.405 Transition = 4.621 ± 1.173 Post = 8.893 ± 1.687 $F_{2,47}$ = 1.409, p = 0.255	Base = 6.853 ± 2.210 Transition = 4.490 ± 1.996 Post = 10.323 ± 2.819 $F_{2,47}$ = 1.530, p = 0.228
Tiram	Base = 0.938 ± 0.504 Transition = 2.237 ± 0.813 Post = 5.411 ± 2.331 $F_{2,47}$ = 2.504, p = 0.093 **LSD base-post = 0.035 (+)**	Base = 3.693 ± 2.091 Transition = 3.470 ± 1.497 Post = 2.891 ± 1.032 $F_{2,47}$ = 0.067, p = 0.935	Base = 11.115 ± 3.625 Transition = 2.500 ± 1.015 Post = 7.884 ± 1.622 $F_{2,45}$ = 3.034, p = 0.059 **LSD base-trans = 0.018 (-)**
Kera	Base = 12.827 ± 6.158 Transition = 1.683 ± 0.795 Post = 2.472 ± 1.088 $F_{2,47}$ = 2.920, p = 0.064 **LSD base-trans = 0.036 (-)**	Base = 4.106 ± 1.234 Transition = 4.923 ± 1.425 Post = 3.771 ± 1.107 $F_{2,47}$ = 0.220, p = 0.803	Base = 5.187 ± 2.272 Transition = 3.899 ± 1.541 Post = 4.704 ± 1.580 $F_{2,46}$ = 0.128, p = 0.881

Table 11(b) continued

Merah	Base = 20.706 ± 5.076 Transition = 17.379 ± 3.392 Post = 18.471 ± 3.166 $F_{2,48}$ = 0.185, p = 0.832	Base = 17.231 ± 4.554 Transition = 27.778 ± 6.457 Post = 15.878 ± 4.293 $F_{2,46}$ = 1.577, p = 0.218	Base = 17.656 ± 3.430 Transition = 17.496 ± 3.873 Post = 20.816 ± 4.231 $F_{2,46}$ = 0.232, p = 0.794

Figure 5(c) Significant changes in Tiram's locomotion

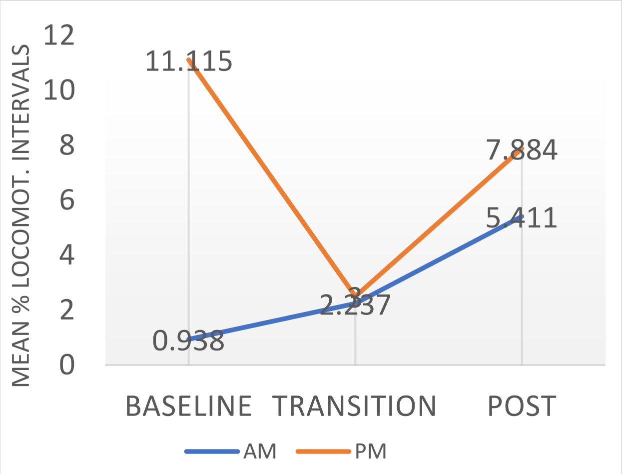
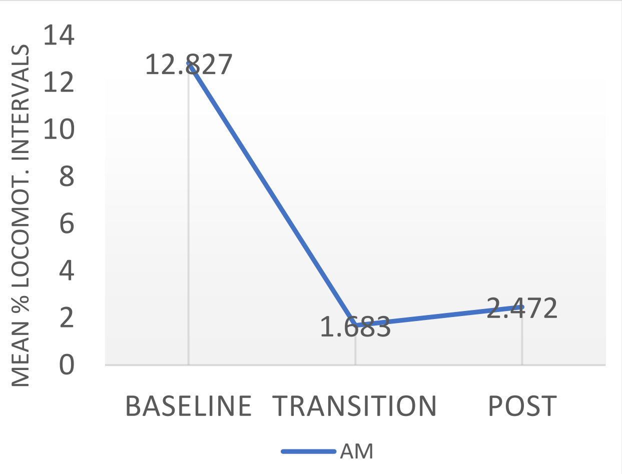


Figure 5(d) Significant changes in Kera's locomotion



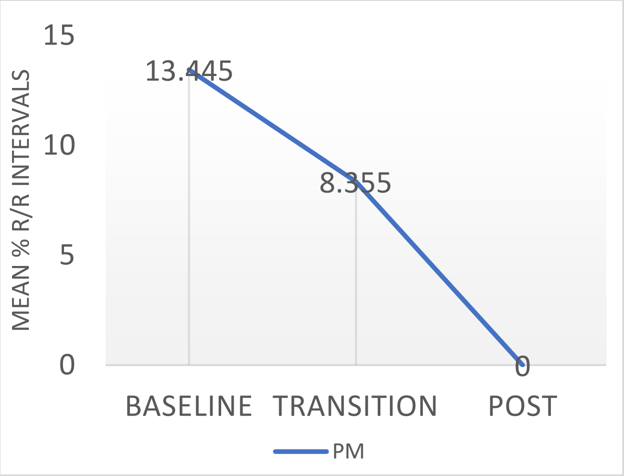
Regurgitation and reingestion

Kera was the only subject who engaged in R/R (see Table 11c). Kera never exhibited the behavior in the morning, but her R/R decreased in the evening of the post phase relative to baseline (Figure 5e).

Table 11(c) Percent of intervals R/R

SUBJECT	AM	MID	PM
Kera	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 0.000 ± 0.000 $F_{2,47}$ = n/a, p = n/a	Base = 2.343 ± 1.491 Transition = 9.643 ± 4.900 Post = 1.250 ± 1.250 $F_{2,47}$ = 2.247, p = 0.117	Base = 13.445 ± 5.360 Transition = 8.355 ± 4.752 Post = 0.000 ± 0.000 $F_{2,46}$ = 2.538, p = 0.091 **LSD base-post = 0.030 (-)**

Figure 5(e) Significant changes in Kera's R/R



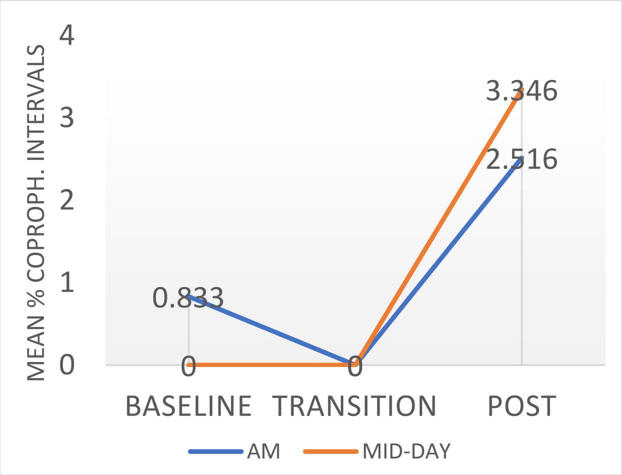
Coprophagy

Kera was the only subject to show a significant change in coprophagy (see Table 11d). Occurrence of the behavior increased in the morning of the post phase and the mid-day of the transition and post phases (Figure 5f).

Table 11(d) Percent of intervals coprophagy

SUBJECT	**AM**	**MID**	**PM**
Kayla	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 2.566 ± 1.753 $F_{2,47}$ = 2.141, p = 0.129	Base = 0.368 ± 0.368 Transition = 0.313 ± 0.313 Post = 0.625 ± 0.625 $F_{2,47}$ = 0.134, p = 0.875	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 6.579 ± 5.096 $F_{2,47}$ = 1.667, p = 0.200
Tiram	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 1.316 ± 1.316 $F_{2,47}$ = 1.000, p = 0.376	Base = 0.000 ± 0.000 Transition = 0.313 ± 0.313 Post = 0.625 ± 0.625 $F_{2,47}$ = 0.600, p = 0.553	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 0.000 ± 0.000 $F_{2,45}$ = n/a, p = n/a
Kera	Base = 0.833 ± 0.833 Transition = 0.000 ± 0.000 Post = 2.516 ± 1.210 $F_{2,47}$ = 2.284, p = 0.114 **LSD trans-post = 0.042 (+)**	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 3.346 ± 1.854 $F_{2,47}$ = 3.258, p = 0.048 **LSD base-post = 0.032 (+)** **LSD trans-post = 0.032 (+)**	Base = 0.694 ± 0.694 Transition = 0.000 ± 0.000 Post = 3.333 ± 3.333 $F_{2,46}$ = 0.853, p = 0.433
Merah	Base = 0.000 ± 0.000 Transition = 0.294 ± 0.294 Post = 1.875 ± 1.573 $F_{2,48}$ = 1.219, p = 0.305	Base = 0.000 ± 0.000 Transition = 0.000 ± 0.000 Post = 0.000 ± 0.000 $F_{2,46}$ = n/a, p = n/a	Base = 0.000 ± 0.000 Transition = 0.329 ± 0.329 Post = 4.314 ± 4.314 $F_{2,46}$ = 0.988, p = 0.380

Figure 5(f) Significant changes in Kera's coprophagy



Social

Kera and Merah both showed significant changes in social behavior (see Table 11e). As shown in Figure 5g, Kera's social behaviors increased in the evening of the post phase relative to baseline. Merah showed a decrease in social behavior in the morning throughout the study (Figure 5h).

Table 11(e) Percent of intervals social

SUBJECT	AM	MID	PM
Kayla	Base = 4.276 ± 4.276 Transition = 0.000 ± 0.000 Post = 0.000 ± 0.000 $F_{2,47}$ = 1.000, p = 0.376	Base = 0.313 ± 0.313 Transition = 1.563 ± 0.992 Post = 0.938 ± 0.680 $F_{2,47}$ = 0.759, p = 0.474	Base = 3.882 ± 2.608 Transition = 5.441 ± 2.939 Post = 1.1222 ± 0.618 $F_{2,47}$ = 0.908, p = 0.411
Tiram	Base = 0.313 ± 0.313 Transition = 4.063 ± 3.422 Post = 3.705 ± 2.590 $F_{2,47}$ = 0.694, p = 0.505	Base = 1.926 ± 1.290 Transition = 2.500 ± 1.646 Post = 0.000 ± 0.000 $F_{2,47}$ = 1.177, p = 0.318	Base = 10.504 ± 5.184 Transition = 2.500 ± 1.872 Post = 10.740 ± 4.738 $F_{2,45}$ = 1.108, p = 0.339
Kera	Base = 14.206 ± 6.798 Transition = 3.438 ± 3.438 Post = 3.750 ± 2.350 $F_{2,47}$ = 1.773, p = 0.181	Base = 10.076 ± 6.326 Transition = 17.439 ± 7.686 Post = 14.839 ± 6.515 $F_{2,47}$ = 0.296, p = 0.746	Base = 0.938 ± 0.680 Transition = 1.941 ± 1.054 Post = 7.667 ± 3.480 $F_{2,46}$ = 3.044, p = 0.058 **LSD base-post = 0.026 (+)**

Table 11(e) continued

Merah	Base = 41.019 ± 9.054 Transition = 17.978 ± 6.138 Post = 13.235 ± 5.768 $F_{2,48} = 4.311$, p = 0.019 **LSD base-trans = 0.026 (-)** **LSD base-post = 0.009 (-)**	Base = 30.700 ± 9.187 Transition = 23.625 ± 8.513 Post = 21.360 ± 6.100 $F_{2,46} = 0.375$, p = 0.689	Base = 25.683 ± 7.942 Transition = 15.431 ± 5.512 Post = 12.646 ± 3.959 $F_{2,46} = 1.266$, p = 0.292

Figure 5(g) Significant changes in Kera's social

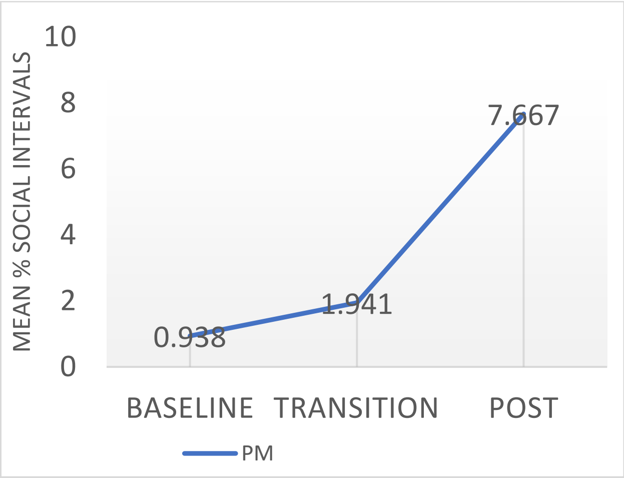
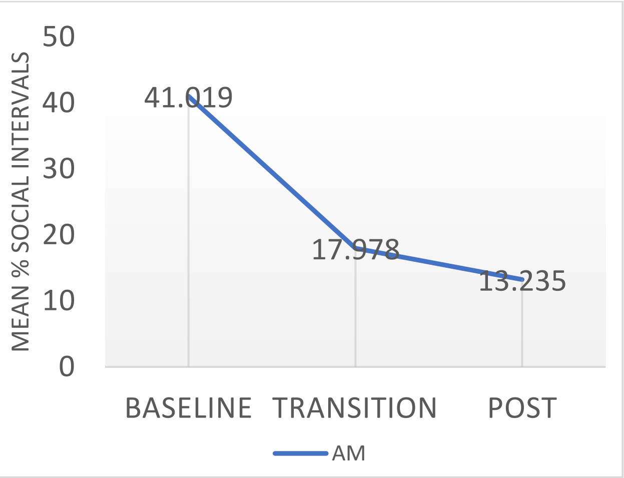


Figure 5(h) Significant changes in Merah's social



Nurse

As nursing is a maternal activity, only Kera and Merah have measures of this behavior (see Table 11f). Merah increased nursing behaviors in the mid-day period of the post phase relative to transition, and in the evening with an increase between the base and transition phases, and a subsequent decrease between the transition and post phases (Figure 5i).

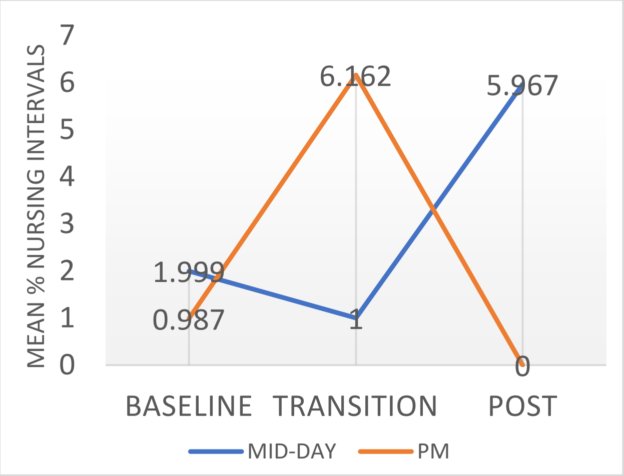
Table 11(f) Percent of intervals nursing

SUBJECT	AM	MID	PM
Kera	Base = 0.658 ± 0.658 Transition = 0.000 ± 0.000 Post = 0.313 ± 0.313 $F_{2,47} = 0.612$, p = 0.546	Base = 1.319 ± 0.903 Transition = 3.750 ± 2.165 Post = 3.125 ± 2.183 $F_{2,47} = 0.465$, p = 0.631	Base = 0.625 ± 0.625 Transition = 2.286 ± 1.068 Post = 1.333 ± 0.909 $F_{2,46} = 0.904$, p = 0.412

Table 11(f) continued

Merah	Base = 0.893 ± 0.893 Transition = 4.468 ± 2.549 Post = 3.436 ± 1.348 $F_{2,48}$ = 1.063, p = 0.354	Base = 1.999 ± 1.372 Transition = 1.000 ± 0.724 Post = 5.967 ± 2.325 $F_{2,46}$ = 2.567, p = 0.088 **LSD trans-post = 0.039 (+)**	Base = 0.987 ± 0.987 Transition = 6.162 ± 2.335 Post = 0.000 ± 0.000 $F_{2,46}$ = 4.917, p = 0.012 **LSD base-trans = 0.017 (+)** **LSD trans-post = 0.006 (-)**

Figure 5(i) Significant changes in Merah's nursing



Other active

This behavior category encompasses all interval behaviors listed in the ethogram that were not analyzed individually (attention, manipulating object, self-directed, yawning, elimination, and chewing). These behaviors were less relevant to the research questions, and were thus collapsed into a single category for analysis (see Table 11g). Tiram showed increases in this category in the mid-day period of the transition and post phases (Figure 5j). Kera had an increase in this category in the morning of the post phase relative to transition and during mid-day of the transition and post phases (Figure 5k).

Table 11(g) Percent of intervals other active

SUBJECT	AM	MID	PM
Kayla	Base = 3.052 ± 1.200 Transition = 10.691 ± 5.502 Post = 6.941 ± 2.092 $F_{2,47}$ = 1.213, p = 0.307	Base = 18.776 ± 5.301 Transition = 12.656 ± 6.001 Post = 22.453 ± 5.835 $F_{2,47}$ = 0.748, p = 0.479	Base = 10.750 ± 5.557 Transition = 19.523 ± 8.18 Post = 19.775 ± 6.626 $F_{2,47}$ = 0.562, p = 0.574
Tiram	Base = 13.984 ± 4.056 Transition = 18.470 ± 7.965 Post = 13.365 ± 5.080 $F_{2,47}$ = 0.220, p = 0.803	Base = 11.661 ± 5.317 Transition = 17.237 ± 7.443 Post = 37.500 ± 7.678 $F_{2,47}$ = 3.889, p = 0.028 **LSD base-post = 0.011 (+)** **LSD trans-post = 0.043 (+)**	Base = 22.555 ± 6.080 Transition = 29.643 ± 7.604 Post = 20.674 ± 6.333 $F_{2,45}$ = 0.468, p = 0.618
Kera	Base = 16.694 ± 5.377 Transition = 23.795 ± 9.542 Post = 75.700 ± 6.884 $F_{2,47}$ = 18.604, p = 0.000 **LSD trans-post = 0.000 (+)**	Base = 14.376 ± 4.971 Transition = 25.335 ± 6.599 Post = 47.177 ± 9.277 $F_{2,47}$ = 5.421, p = 0.008 **LSD base-post = 0.002 (+)** **LSD trans-post = 0.037 (+)**	Base = 49.231 ± 9.202 Transition = 52.716 ± 8.241 Post = 58.630 ± 8.262 $F_{2,46}$ = 0.300, p = 0.742
Merah	Base = 29.838 ± 6.410 Transition = 32.206 ± 6.453 Post = 33.671 ± 5.634 $F_{2,48}$ = 0.096, p = 0.909	Base = 37.393 ± 6.503 Transition = 30.383 ± 6.730 Post = 28.706 ± 3.880 $F_{2,46}$ = 0.639, p = 0.523	Base = 48.058 ± 7.303 Transition = 37.039 ± 5.317 Post = 40.870 ± 6.119 Mean = 42.013 ± 3.627 $F_{2,46}$ = 0.802, p = 0.455

Figure 5(j) Significant changes in Tiram's other active

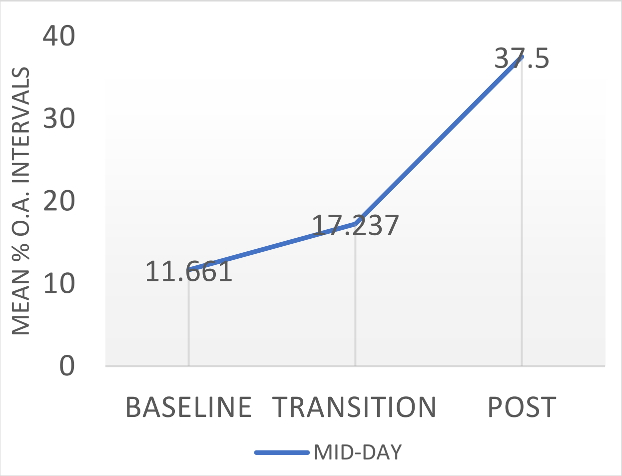
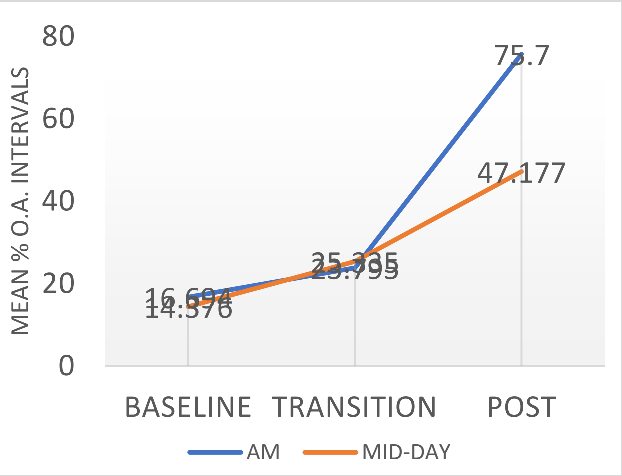


Figure 5(k) Significant changes in Kera's other active



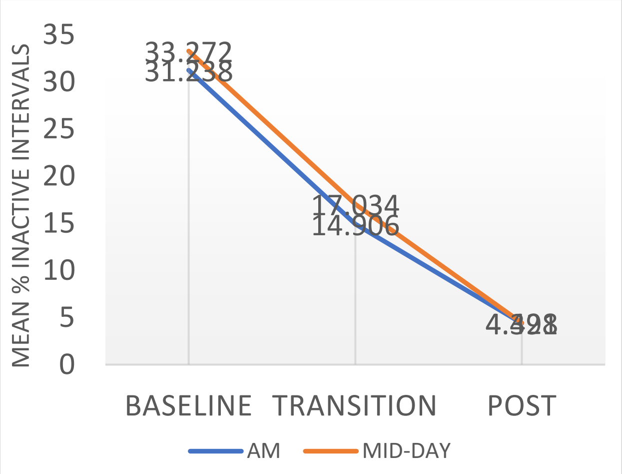
Inactive

Kera was the only subject to show a significant change in inactivity (Table 11h). Her inactivity decreased in the mid-day period of the post phase relative to baseline (Figure 5l).

Table 11(h) Percent of intervals inactive

SUBJECT	AM	MID	PM
Kayla	Base = 66.510 ± 10.004 Transition = 41.398 ± 11.143 Post = 40.230 ± 11.359 $F_{2,47} = 1.872$, p = 0.166	Base = 47.728 ± 10.062 Transition = 43.851 ± 10.689 Post = 32.710 ± 6.829 $F_{2,47} = 0.696$, p = 0.504	Base = 30.616 ± 8.692 Transition = 48.010 ± 10.386 Post = 23.104 ± 6.800 $F_{2,47} = 2.132$, p = 0.130
Tiram	Base = 64.531 ± 8.102 Transition = 47.878 ± 9.763 Post = 41.104 ± 9.764 $F_{2,47} = 1.701$, p = 0.194	Base = 59.704 ± 9.856 Transition = 50.313 ± 10.719 Post = 43.672 ± 8.705 $F_{2,47} = 0.676$, p = 0.514	Base = 38.675 ± 8.028 Transition = 54.286 ± 9.748 Post = 33.081 ± 6.853 $F_{2,45} = 1.734$, p = 0.189
Kera	Base = 31.238 ± 7.168 Transition = 14.906 ± 6.709 Post = 4.391 ± 2.495 $F_{2,47} = 5.351$, p = 0.008 **LSD base-post = 0.002 (-)**	Base = 33.272 ± 9.501 Transition = 17.034 ± 6.565 Post = 4.428 ± 1.919 $F_{2,47} = 4.577$, p = 0.016 **LSD base-post = 0.004 (-)**	Base = 9.376 ± 3.547 Transition = 20.354 ± 7.736 Post = 15.333 ± 5.243 $F_{2,46} = 0.918$, p = 0.407
Merah	Base = 2.790 ± 1.455 Transition = 4.385 ± 1.747 Post = 7.051 ± 4.101 $F_{2,48} = 0.635$, p = 0.534	Base = 3.192 ± 1.379 Transition = 1.388 ± 0.616 Post = 4.468 ± 2.329 $F_{2,46} = 0.885$, p = 0.420	Base = 2.969 ± 1.275 Transition = 8.520 ± 2.916 Post = 3.837 ± 1.491 $F_{2,46} = 2.154$, p = 0.128

Figure 5(l) Significant changes in Kera's inactivity



Serum Biomarkers

Tiram provided three serum samples, one from each phase (baseline, transition, and post). Kayla provided two serum samples, one during the baseline phase and one during post. All raw values for the serum biomarkers from each individual are listed in Table 12.

Triglycerides

Tiram's triglycerides increased by 20% from the baseline to transition phases, but decreased by 28% between the transition and biscuit-free conditions. From the initial to final collection, Tiram's triglycerides decreased by 13%. Kayla's triglycerides increased by 38% between her two samples.

Cholesterol

The change in Tiram's total cholesterol was negligible. It decreased by 2% between the baseline and transition phases, increased by 6% between the transition and biscuit-free conditions, and increased by 3% from the initial to final collection. Kayla's total cholesterol decreased by 13% between her two samples.

Insulin and glucose

Tiram and Kayla both showed a substantial decrease in insulin and the insulin:glucose ratio from the baseline to the post phase. Tiram's insulin decreased by 22% between the baseline and transition phases, and 37% between the transition and biscuit-free phases. From initial to final serum collection, Tiram's insulin decreased by a total of 51%. His glucose increased by 8% from the baseline to the transition, but decreased by 10% from transition to biscuit-free. From initial to final collection, Tiram's glucose increased by 19%. His insulin:glucose ratio decreased by 29% from baseline to transition, and by 43% between transition and biscuit-free phase. From initial to final collection, Tiram's insulin:glucose ratio decreased by 59%. Between her two samples, Kayla’s insulin level decreased by 73%, her glucose level decreased by 43%, and her insulin:glucose ration decreased by 52 %.

Leptin

Tiram’s leptin level increased by 67% between the baseline and transition phases, but decreased by 80% from the transition to biscuit-free condition. From the initial to final sample, his circulating leptin decreased by 66%. Kayla’s leptin decreased by 40% between her two samples.

Table 12 Changes in serum biomarker levels

Subject	Phase	Triglycerides mg/dL	Total Cholesterol mg/dL	Insulin mU/L	Glucose mg/dL	Insulin:Glucose ratio	Leptin ng/mL
Tiram	Base	106	181	10.723	83	0.129	19.01
Tiram	Trans	127	177	8.315	90	0.092	31.83
Tiram	Post	92	187	5.215	99	0.053	6.44
Kayla	Base	89	181	22.216	105	0.210	44.87
Kayla	Post	123	156	6.08	60	0.101	26.92

CHAPTER 4

DISCUSSION

Overview

The present study examined the effects of dietary manipulation on the behavioral and physical wellbeing of captive orangutans. The goal of the manipulation was to better mimic wild nutrition by eliminating commercial biscuits from the diet and increasing fiber content. Proposed hypotheses were that this manipulation would, ultimately lead to (1) increased time spent feeding, (2) increased active time, a more diverse space use pattern, and decreased undesirable behaviors, and (3) improved health parameters as evidenced by a decrease in the measured serum biomarkers. Some results of this study supported these initial hypotheses, while others call for further investigation.

Behavior

In two studies with similar methodology, a reduced-biscuit diet increased locomotion but not time spent feeding in orangutans (Cassella 2012), and a biscuit-free diet increased feeding behavior in gorillas (Less, 2012). In the present study, only Merah (the adolescent subject) showed an increase in both feeding behavior and locomotion. However, it should be considered that biscuits were not entirely eliminated from Merah’s diet. Tiram and Kayla (the adult male and older adult female) also showed increased locomotion, but no change in feeding behavior.

It may be that the low-starch diet caused metabolic changes that stimulated increased activity, but that too much of it was fed off-exhibit to statistically observe any on-exhibit change in feeding behavior. However, why the younger adult female, Kera, did not show a statistical increase in locomotion remains unexplained.

It is relevant to compare the results of the present study to those of Cassella (2012) because she implemented a similar diet change with three of the same subjects (Tiram, Kayla, and Kera) at the Cleveland Metroparks Zoo. She reduced, but did not eliminate, biscuits, and specifically targeted Tiram and Kayla for weight loss. Her results supported the hypothesis that weight loss would be associated with increased time spent in the elevated levels of the exhibit. She also reported increased locomotion and suggested that this may have been due to metabolic changes, or could have been a demonstration of food-seeking behavior in response to the sudden diet change. We attempted to lessen the severity of the diet change in the present experiment by adding the transition period. However, as we eliminated the biscuits entirely, the subjects may have still been exhibiting food-seeking behaviors because of dissatisfaction with the other changes.

Cassella also found that all subjects increased their use of the highest enclosure level. This was not entirely the case in the present study, as only Kera and Merah increased time spent in the tree. This may be due to Cassella's goal of targeted weight loss for Tiram and Kayla. In her study, both subjects were on reduced-calorie diets, and lost 32 and 21 pounds, respectively. The present study was not designed to encourage weight loss, and, while some weight loss did occur, if the loss was less drastic, this may have contributed to the lack of increased tree use for Tiram and Kayla.

The inconsistency of this finding with Cassella's is not necessarily undesirable. The goal of the present study was not to increase use of elevated space, but for subjects to diversify their space use patterns by showing significant change in use of the various levels. While there was not a consistent increase in use of elevated space for the entire group, all subjects did show significant changes in their individual space-use patterns. As such, the hypothesis that subjects would demonstrate a more diverse space-use pattern was supported.

Undesirable behaviors in captive great apes are problematic for both health and conservation. The stomach acid regurgitated during R/R can harm the esophageal tract and cause dental acid erosion (Hill, 2009; Lowenstine et al., 2016), and coprophagy can contribute to the spread of disease (Zimmermann et al., 2011). Further, these behaviors are unpleasant for zoo guests to witness. As naturalistic exhibits have been demonstrated to improve public attitudes toward African apes (Lukas & Ross, 2014), reducing undesirable behaviors and, thus, more accurately representing natural orangutan behavior, may improve public interest in conservation.

There are many hypotheses for the cause of regurgitation and reingestion (R/R). Some studies suggest behavioral and welfare-based causes, for example boredom, stress, lack of foraging materials or social stimulation (Struck et al., 2007). However, there is also strong evidence for dietary triggers like inconsistent or reduced feeding, and low-fiber diets, as demonstrated by the elimination of R/R from a group of gorillas after biscuit elimination (Less, 2012; Struck et al., 2007). Given the range of hypotheses in the literature, the true cause of the behavior is likely a combination of behavioral welfare and dietary content. This is maintained in the present study, as only one subject – Kera – engaged in the behavior, despite all subjects being on the same diet. While this hypothesis is currently unsupported in the literature, this suggests that R/R may be an individualistic behavior that is promoted or diminished by certain diets. That is, the content of diet may enable regurgitation, but only if it is already a part of the animal's behavior pattern. While the true cause of R/R remains unknown, Kera's frequency of R/R did decrease, but was not eliminated, in the biscuit-free condition of the present study.

Coprophagy is also undesirable for health and conservation reasons, but, given that bonobos have practiced coprophagy in the wild in times of food scarcity (Sakamaki, 2010), it is less unnatural than R/R, and short-term occurrence may be reasonable in this experimental design. Coprophagy was rare in this group before the diet manipulation and although Kera was the only individual whose coprophagy increased significantly, it did increase to some degree in all subjects. Previous studies with orangutans and gorillas have also reported an increase in coprophagy after biscuit reduction (Cassella, 2012; Less, 2012), therefore, this may be an adaptive response to what the subjects are interpreting as a food shortage.

The decrease in R/R, but increase in coprophagy, reported here may be evidence for the hypothesis that diet change does interfere with the ability to regurgitate. If the increase in coprophagy is a response to the diet change, it may decrease over time as the subjects adjust to the diet. Further study into the long-term persistence of undesirable behaviors after a decrease in dietary starch, along with their implications for health and conservation, is advised.

Many of the modifications made to optimize the biscuit-free diet were due to concerns about Kera's weight. She was a particularly "picky" eater, but it is also notable that Merah showed a significant increase in nursing behavior in the transition phase. The first instance of concern about Kera's weight came on October 10, during the first week of the biscuit-free phase. Thus, some of her weight loss may have been related to the increased nursing, which is related to weight loss in human mothers (Dewey et al., 1993).

Lastly, in terms of behavior, the present study did not support the previous finding that biscuit reduction increased inactivity in orangutans (Cassella, 2012). There was no significant change in percent of intervals scored “inactive”, except for Kera. Her inactivity decreased, but only as an inverse of an increase in the “other active” category. This was likely driven by her increase in “chewing” behavior, wherein she sat immobile and masticated. Thus, she may not have been ‘inactive’, but was still immobile and idle, so this statistical decrease in inactivity may be misleading.

Health

From a health perspective, this diet change successfully improved insulin, insulin:glucose ratio, and leptin levels. As orangutans are particularly susceptible to glucose-regulation problems (Gresl et al., 2000), the improvement of insulin:glucose ratio was encouraging. The reported results for cholesterol (Tiram’s negligible increase, Kayla’s small decrease), and triglycerides (Tiram’s small decrease, Kayla’s substantial increase) contrasted with expectations given the effects of high-fiber diets in humans (Ludwig et al., 1999). However, one analysis of dietary fiber did show that, while significant, effect on total cholesterol was small (Brown et al., 1999). If the effect on cholesterol is slight, the sample size of this study may have been too small to detect a significant change. Further, a stronger effect may have been revealed by examining levels of HDL and LDL cholesterol independently, as this is a more precise measure than total cholesterol alone (Gordon et al., 1977). As all levels of total cholesterol and triglycerides reported here are higher than reported levels in free-ranging orangutans (Schmidt et al., 2006), any decrease is indicative of a positive change in the health of these subjects.

The present findings were somewhat consistent with what has been reported in gorillas. Less (2012) found that a biscuit-free diet with resistant starch similarly decreased insulin and improved the insulin:glucose ratio, but differed in its decrease in cholesterol, increased in triglycerides, and lack of effect on leptin. In Less' study, the biscuit-free diet alone did not decrease cholesterol in gorillas, but adding resistant starch did. This was not the case in the present study, as Tiram's cholesterol was lowest in the transition phase, before resistant starch was added. Further, why Tiram's triglycerides decreased while Kayla's increased is unclear. The only difference between the diet items of these two subjects was the presence of a chia seed mixture for Kayla, which has been shown to have no direct effects on triglycerides in humans (Nieman et al., 2009).

It is also unclear why leptin levels decreased so substantially in the present study, while they were unaffected in gorillas. However, as high-fiber diets do tend to decrease leptin in human subjects (Murakami et al., 2009), the results of the present study seem more logical given the experimental design. The discrepancy may be related to a difference between the species' natural responses to the biscuit-free diet as, while orangutans are primarily frugivorous, gorillas are herbivorous. Thus, these similar diets may have different effects on their lipid profiles.

Conclusion

In conclusion, the present study had three goals: to (1) increase time spent feeding (2) decrease time spent inactive, diversify space use, and decrease undesirable behaviors, and (3) improve serum biomarkers to indicate a healthier weight and lowered risk of cardiovascular and respiratory diseases. Hypothesis 1 was not supported, but this may be due to the restriction of behavioral observations to on-exhibit activity. The final diet included daily on-exhibit scatter feedings, but much feeding was also done off-exhibit. Hypothesis 2 was partially supported by a more diverse space-use pattern in all subjects, and the decrease of R/R in Kera. However, the goal of decreased inactivity was not met, and an increase in coprophagy prevented the conclusion that undesirable behaviors decreased. Hypothesis 3 was also partially supported. Insulin, leptin, and the insulin:glucose ratio improved, but cholesterol and triglycerides were each only improved in one subject.

Future Directions

Studying the effect of nutrition on health and behavior in captive primates is relatively new, especially in orangutans. As such, humans and other apes are currently the most effective comparison by which to estimate healthy change (Less, 2012). More extensive studies with larger groups will be vital in establishing what is normal in terms of health markers, defining obesity, and determining what normal behavior patterns look like for orangutans in captivity. This study attempted to define those parameters, but in a case study-type design, due to the small sample group, and even smaller set of serum samples. These small-scale data may be useful in guiding the development of future studies with larger samples.

Future studies may benefit from adding some sort of novel enrichment program to the proposed diet change. This type of program could encourage the use of varying exhibit areas, and, through mental stimulation and encouragement to exercise, would likely be beneficial to the subjects' overall wellbeing. When paired with a biscuit-free diet, this could strengthen the positive effects on health and behavior observed in this study. Further, this may alter results to support some of the hypotheses that remained unsupported at the end of this study. Time spent inactive may decrease when there are novel objects to manipulate, and the decrease of unoccupied time may lessen the undesirable behaviors that may be related to boredom. This could also improve attitudes of the public toward the animals and, consequently, conservation efforts, as zoo guests rate exhibits more favorably when animals are active and enriched (Tripp, 1985).

It will also be useful for any future replication to refine the method used to quantify feeding behavior. The present study relied on time spent feeding, but ingestion rate varies by individual and type of food (Zinner, 1999). Thus, weighing food given to animals and subsequently weighing the food not eaten, may provide a more accurate measure for actual amount of food ingested. Lastly, future studies may consider extending observations for a longer period after the diet change. This would provide the subjects more time to adjust to the diet, and allow the researcher to determine the long-term effects of the change once normalized. In this condition, coprophagy may decrease, and the effects of feeding a diet with a more natural nutritional makeup may become clearer. By creating an environment where captive animals can feel and behave more like their wild counterparts, the lives of the captive animals themselves, and the conservation efforts for their endangered species, will be improved.

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