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THE ENERGETIC AND NUTRITIONAL COSTS OF MOTHERHOOD IN WILD BORNEAN
ORANGUTANS

By

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ABSTRACT OF THE DISSERTATION

The energetic and nutritional costs of motherhood in wild Bornean orangutans

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Lactation is the most energetically expensive part of reproduction for female mammals, and species utilize different strategies to overcome these energetic costs. Mother orangutans exhibit multiyear lactation and have the longest lactational period of any mammal, with infants nursing for up to eight years spanning multiple unpredictable fruiting cycles. Still, there is little research on how mothers are able to raise an infant over the course of multiple years. The main goal of this dissertation is to examine the behavioral strategies and consequent physiological responses that mother orangutans use to maximize fitness across periods of infant development. Specifically, I seek to determine 1) if a mother modifies her daily activity, dietary composition, and nutritional intake throughout infant development, 2) how the energetic condition of a mother varies across infant development, and 3) how a mother who lactates across multiple years maintains homeostasis in a relatively marginal and variable energetic environment.

In Chapter Two, I explore mother orangutan behavior by investigating if there is variation in a mother's activity and feeding behavior. I find that a mother in higher fruiting periods utilizes a strategy that maximizes food intake, especially ripe fruit, while in lower fruiting periods she minimizes her activity to conserve energy while feeding more on non-fruit items. In Chapter Three, I analyze a mother's caloric and

macronutrient intake estimates based on nutritional analyzes of orangutan food items and apply the Geometric Framework of Nutrition to determine if a mother is prioritizing a specific ratio of macronutrients. I find that when a mother has a young infant, she increases her caloric and carbohydrate intake during periods of high fruit available, but cannot do this during low fruit periods and has a much reduced caloric intake. Additionally, during high fruit periods, a mother consumes a similar macronutrient ratio regardless of infant age, and this ratio is potentially the best ratio to build up fat reserves. In Chapter Four, I analyze urinary biomarkers to determine how a mother's energetic condition varies across her lactation period, and I show that overall, a mother is in her worst energetic condition while she has a young infant during periods of low fruit availability. Collectively, these chapters demonstrate that the greatest period of maternal care in orangutans is while a mother has a two-year-old infant, especially in low periods of fruit availability.

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Chapter 1. Introduction

Research focusing on life-history evolution has revealed that primates have extended life histories relative to other mammalian species of similar body mass, including longer gestation and lactation periods, and extended periods of juvenile dependency (Lee 1987, Emery Thompson 2013a, Pontzer et al. 2014). Therefore, it is likely that primate mothers, particularly those with multi-year lactation spanning periods of unpredictable food availability like orangutans (van Noordwijk et al. 2013b), will have a suite of behavioral and physiological adaptations to cope with the long-term energetic demands of motherhood, while minimizing extrinsic risk to her developing infant. To nourish her offspring through gestation and lactation, and maintain energy homeostasis, primate mothers use a variety of strategies to compensate for this additional energetic burden, including targeting foods with an optimal balance of nutrients, modifying activity levels, and using stored fat reserves and/or skeletal muscle for energy (Brockman and van Schaik 2005, van Noordwijk 2012, Vogel et al. 2012b). However, little is known about 1) how wild mother primates modulate their diet and behavior to buffer their infants from variable energy availability in the habitat and support the additional costs associated with gestation and lactation, 2) if they experience energy deficits during infant development, and 3) how this may relate to their extended life histories. The objective of this thesis is to explore these areas to gain a better understanding of maternal strategies in one of our closet living relatives, the orangutan (*Pongo sp.*).

Orangutans have a suite of key characteristics that separate them from other primates, making them an ideal species for a study of motherhood and nutritional

strategies, and below, I explore these characteristics. Perhaps most noticeably, orangutans are the only ape to feature primarily solitary foraging and feeding (except for mother-infant pairs), enabling researchers to investigate ecological questions without as many confounding social factors found in the other gregarious great apes. For instance, in the fission-fusion social structure of chimpanzees, the presence of other individuals directly impacts the feeding behavior of both individuals and groups of individuals (Wrangham and White 1988). Orangutans in the wild also have very diverse diets (Morrogh-Bernard et al. 2009, Vogel et al. 2015, 2017), build fat reserves during periods of fruit abundance (Knott 1998, Wich et al. 2006), and catabolize these reserves when preferred fruit is scarce and caloric intake is reduced (Knott 1998, Harrison et al. 2010). This pattern is not observed in other ape species and has been hypothesized as vital in the evolution of human reproductive regulation (Wells 2006), especially since humans devote a greater percentage of energy to reproduction than other hominoids (Reiches et al. 2009). These factors, in conjunction with a diverse diet that requires years of learning (Jaeggi et al. 2008, 2010), existence in an unpredictable and potentially low-quality habitat (Vogel et al. 2012b), and extremely long periods of juvenile dependency, make their potential cost of motherhood great (van Noordwijk et al. 2013b).

1.1 Orangutan Habitat

Across the islands of Borneo and Sumatra, orangutans exist in three main habitat types: 1) peat-swamp forest, 2) dipterocarp-dominated limestone-karst forests, and 3) masting dipterocarp-dominated dryland forests (Husson et al. 2009). Each habitat type can be subdivided into areas with similar soil structures, rainfall, phenology, and nutrient

availability, influencing the density and behavioral ecology of the residing orangutan populations (van Schaik et al. 1993, Wich and Schaik 2000, Husson et al. 2009, Vogel et al. 2015). Flowering and fruiting events, in particular, affect orangutan ranging, condition, reproduction, and behavior (Singleton and Van Schaik 2001, Buij et al. 2002, Harrison et al. 2010, 2016). While in many mammalian species the amount of food in a habitat influences the density of populations, in orangutans population density is thought to be limited by the length and severity of food shortages (Marshall and Leighton 2006, Marshall et al. 2009). At the largest scale of orangutan distribution, there are major differences in the soil structure and consequently plant phenology between the islands of Sumatra and Borneo (Wich et al. 2011). Borneo has less fertile soils than Sumatra as a result of older volcanic activity (MacKinnon et al. 1996), leading to lower forest productivity and a mean difference in percent fruiting trees between the islands ranging from 6.08% - 23.84% depending on habitat type (Wich et al. 2011). Additionally, Bornean forests, on average, have fewer months per year where trees fruit (Marshall et al. 2009), leading to smaller orangutan densities across habitats (Husson et al. 2009). When compared against Sumatran peat-swamp forests, Bornean peat-swamp forests (which are the focal habitat of this project) have the largest mean difference in percent fruiting trees (23.84%; Wich et al., 2011), fewer months annually with high fruit availability (Marshall et al. 2009), and the greatest mean difference in orangutan densities (Husson et al. 2009).

Overall, peat-swamp forests contain the highest orangutan densities and largest populations (Morrogh-Bernard et al. 2003, Wich et al. 2008, Husson et al. 2009), though populations are declining at an alarming rate (Cattau et al. 2015). In Kalimantan (Indonesian Borneo), peat-swamp forests have less pronounced variation fruit availability

than other habitat types (Wich et al. 2011). Factors affecting peat-swamp forest structure, productivity, and subsequently phenology include peat depth and water retention (Page et al. 1999, 2011). Kalimantan peat-swamp forests are older than many other Asian peatlands, forming over 10,000 years ago (Rieley et al. 1992), and are mainly ombrogenous forests, meaning they acquire water and nutrients from aerial sources (Page et al. 1999), with varying degrees of nutrients arriving through rheotrophism (supplied by flowing water; Yustinus, 2005; Osaki et al., 2017). The degree of rheotrophism, in conjunction with peat depth, leads to differences in the phenology of food trees for orangutans across the landscape (Vogel et al. 2015, Harrison et al. 2016), presenting individuals with an unpredictable seasonality. The Tuanan Research Station, where this study was conducted, is located in a peat-swamp forest near a major river that supplies an annual flooding regime, increasing the forest productivity, as shown by longer fruiting duration compared to nearby areas (Wich et al. 2009, Harrison et al. 2016). In fact, Tuanan has one of the highest estimated orangutan densities of any field site on Borneo (4.3-4.5 individuals/km²; (van Schaik et al. 2005, Husson et al. 2009). Still, Bornean orangutans are now critically endangered (Ancrenaz et al. 2018), and it is estimated that only 40-45% of the original orangutan population exists in the landscape where Tuanan is located, with overall densities still decreasing (Cattau et al. 2015).

1.2 Bornean Orangutans

Bornean orangutans (*Pongo pygmaeus ssp.*) in peat-swamp forests are an example of a species in a relatively unpredictable habitat. As mentioned before, the peatlands of Kalimantan are characterized by unpredictable seasonality and levels of fruit abundance

(FAI-% of fruiting trees) that rarely exceed more than 14% of trees fruiting at any one time. Thus, orangutans in these habitats are likely faced with higher levels of energetic stress than African apes, which experience greater regularity in fruit availability (van Schaik and Pfannes 2005). Overall, orangutan diets exhibit a much greater range in nutritional intake compared to chimpanzees, and exhibit up to a 5-fold difference in energy intake across seasons (Knott 1998, 2005, Vogel et al. 2015, 2017). Furthermore, there is no correlation between fruiting periods and the timing of births for Bornean orangutans (but potentially with conception for multiparous mothers outside of very low fruit availability; van Noordwijk, personal comm.). Harrison et al. (Harrison et al. 2010) found that energetic state does not relate to fruit availability and individuals often fall into a negative energy balance state in these peat-swamp forests. Conversely, Bornean orangutans in dipterocarp forests, which are masting habitats with unpredictable supra-annual seasonality, increase their fat reserves during the highest of fruiting periods, an adaptation to compensate for lengthy periods of low food availability and potentially help support their aseasonal reproduction (Knott 1998). Taken together, this suggests that orangutans are neither traditional income or capital breeders. Instead, they utilize a hybrid income-capital strategy, where the mother varies her nutritional contribution towards infant development. This variation depends on the availability of high quality foods over an extended period spanning several fruiting seasons, which potentially alters behavioral strategies used to maintain homeostasis while providing the required amounts of macronutrients and energy to her infant.

Orangutans also have the longest interbirth interval (IBI) of any primate, averaging 7.6 years (van Noordwijk et al. 2018), but we lack a clear understanding of

how mothers are able to cope with the energetic costs of nurturing an infant in an unpredictable habitat or why juveniles depend on their mothers for such extended periods (Knott 2001, Jaeggi et al. 2008, van Noordwijk et al. 2018). Given that selection should favor the maximization of fitness, the orangutan's extended IBI most likely increases offspring survival. In fact, orangutans have an average of 94% infant survival (van Noordwijk et al. 2018). Some level of extrinsic mortality of offspring (predation, starvation, disease) is unavoidable, and several hypotheses specify adaptations to minimize mortality. Bet-hedging (Stearns 2000) is a strategy that favors longer life spans and lower reproductive rates when it is costly to reproduce and mortality varies greatly. Ecological risk aversion is another applicable hypothesis, where it is beneficial to slow down development to minimize an infants' risk of predation and starvation (Janson and van Schaik 1993).

Orangutans fit a specialized multi-year lactation model where a mother's energy intake should initially increase after parturition, but level off after her dependent begins ingesting solid food (as early as 12 months old; van Noordwijk et al., 2013). However, the data to support this concept have been based solely on time spent feeding, which may not equate to nutritional intake (Schülke et al. 2006). Humans also exhibit multi-year lactation, but have evolved a strategy where solid food is provisioned at an early age (around 6 months) as a supplement to a mother's relatively constant lactation effort (Kaplan et al. 2000, Butte and King 2005). In fact, a mother orangutan's time spent feeding remains constant throughout the development of her infant (van Noordwijk et al. 2013b), suggesting mothers use other strategies to provide for the changing energetic demands of her offspring. Thus, a mother's dietary strategy will be strongly influenced

by a changing balance of macronutrient requirements throughout lactation and infant development. While the amount of protein in milk remains relatively stable with respect to the mother's diet, milk's energetic content is significantly related to how much energy a mother is able to extract from her food (Hinde and Milligan 2011). We know very little about how mother orangutans regulate their nutritional intake throughout infant and juvenile development, and what strategies they use to meet the energetic demands of her infant.

1.3 Energetics

1.3.1 Energetics and Nutrition

Primates occupy a wide breadth of dietary niches that range from extreme generalist to niche specialist diets. Within these dietary niches, there is great variability in the nutritional composition of foods, even within the same habitat, across time, space, and location within the tree. Most of the energy in primate foods comes from four macronutrients: protein, carbohydrates, lipids, and fiber (Milton 1979, Nagy and Milton 1979, Oftedal et al. 1991, Lambert 2010). The most accessible energy is found in non-protein nutrients (non-protein energy, NPe), particularly carbohydrates and lipids, thus making it easiest to build fat when consumed in excess. Still, protein is essential for growth and development (Schoener 1971, Oftedal et al. 1991, Vogel et al. 2012b), so there exists a tradeoff in food selection between protein rich foods (protein energy, Pe) and NPe. Most preferred foods consumed by orangutans are low in protein (Vogel et al. 2015). Narita et al. (2010) found that orangutans have a proliferation of gene copies that code for protein-digesting enzymes, suggesting protein is limiting and that they have

evolved mechanisms to maximize protein utilization. Compared to other apes, orangutans have the lowest crude protein content in their milk (crude protein: 0.7 ± 0.25) (Hinde and Milligan 2011), but may be able to extract more energy from protein relative to other primates. It remains unknown if mother orangutans target high nutrient foods to meet the energetic demands of the infant while keeping the amount of food intake constant, or if they increase their overall intake to meet the energetic demands of the infant while maintaining a consistent balance of macronutrients.

The Geometric Framework of Nutrition (GF; Simpson et al., 1993) is a useful tool for investigating diet selection in relation to the quantity of nutrients consumed. The GF can be applied to the relevant important nutrients in a system and has helped understand the relationships between nutrition, ecology, physiology, environment, and behavior across species. Research applying the GF has introduced models of multidimensional nutrition to the study of birds (Raubenheimer and Simpson 1997, Schaefer et al. 2003, Köhler et al. 2012), demonstrated that giant pandas consume and absorb an equivalent amount of protein relative to other carnivores despite being obligate herbivores (Nie et al. 2019), and demonstrated the importance of understanding the nutritional consequences of plastic consumption across trophic levels (Machovsky-Capuska et al. 2019). The GF has also been previously used to understand the impact of seasonality on primate behavior and ecology. Diademed sifakas (*Propithecus diadema*) are able to maintain a macronutrient balance across wet and dry seasons even though they shift from fruit to non-fruit resources (Irwin et al. 2014, 2015). Spider monkeys (*Ateles chamek*), meanwhile, maintain a stable protein intake by switching between figs and other ripe fruits, depending on the season (Felton et al. 2009b). Due to its flexibility and simplicity,

the GF is an ideal tool to use for understanding variation in orangutan nutrition across ecological conditions.

1.3.2 Endocrinology and indicators of energetic status

Several non-invasive collection methods using wild primate urine combined with laboratory analyses have been developed to gain a better understanding of energetic and somatic conditions of primates. These laboratory methods include quantifying ketone bodies (Knott 1998), urea, C-peptide of insulin (Sherry and Ellison 2007), and cortisol (Emery Thompson et al. 2010). Ketone bodies are produced when fat reserves are catabolized as a consequence of energy expenditure exceeding energetic intake, known as negative energy balance state (Emery Thompson 2017). Ketone bodies are quantifiable in urine when they oversaturate the bloodstream during carbohydrate shortages (Emery Thompson and Knott 2008). Collectively, previous work utilizing urinary ketone measurements show that Bornean orangutans across habitats excrete ketones during low food availability periods, but that individuals in peat-swamp forests have higher ketone production (Knott 1998, Harrison et al. 2010). The concentration of urea in an individual's urine is an indicator of nitrogen catabolism or metabolism and can be used to determine an individual's body condition (Barboza and Parker 2006, Vogel et al. 2012a, 2012b). Multiple species of arctic ungulate rely on body stores of protein while they are gestating during the winter, and urea has been used to measure body condition change through these periods (Larter and Nagy 2001, Gustine et al. 2012). Another useful method to examine energy balance, with higher sensitivity, is measuring the urinary metabolite of insulin, C-peptide (UCP). Because insulin regulates glucose uptake and the

storage of surplus energy, it provides a sensitive indicator for energy balance (Emery Thompson and Knott 2008). Therefore, by measuring the excretion of an insulin metabolite that tracks the rate of production, like UCP, one can estimate energy balance from urine samples collected in a field setting (Emery Thompson and Knott 2008). For instance, Grueter et al. (2014) found that when female mountain gorillas (*Gorilla beringei beringei*) increased their intake of a highly nutritious but seasonal resource, bamboo, UCP levels rose. This positive relationship was found in both habitats with greater availability of bamboo and during the peak bamboo season. A similar relationship was found in mother mantled howler monkeys (*Alouatta palliata*), where food availability and UCP were positively related (Dias et al. 2018). Emery Thompson et al. (2012a) found that the most intense energetic burden on lactating chimpanzees was during the first 1-2 years using UCP measurements. Glucocorticoids, including cortisol, are hormones that primarily regulate the availability of glucose and are released by the adrenal gland when the homeostasis of an individual is compromised (Saplosky 1992). Because of this, glucocorticoids are ideal hormones to measure nutritional stress in response to deficits in food availability, especially when confounding social stressors are minimized (Emery Thompson 2017). A decrease in fruit availability has led to a significant increase in glucocorticoids in multiple primate species, including species with high rates of folivory (Behie et al. 2010, Emery Thompson et al. 2010, Dias et al. 2017).

Together, these measures can be analyzed in relationship to daily energy and macro-nutrient intake to track changes in energetic status, and can be compared across individuals to examine variation across sex, age, reproductive status, seasonality, and habitat quality. The presence of ketones in conjunction with low levels of urinary C-

peptides, for instance, will demonstrate that an individual has a negative energy balance and is failing to meet energetic goals, even if behavioral measures suggest otherwise. Comparing these data across different periods during lactation will show how a mother is affected by the nutritional strategy she employs.

1.4 Life History

The life history of a species is the manifestation of adaptations to the environment, given phylogenetic constraints, that maximize reproductive success (e.g., fitness) (Harvey and Clutton-Brock 1985). Life history traits are shaped through an interplay between 1) external ecological factors and 2) intrinsic tradeoffs and net developmental costs (Stearns 2000). How does an individual acquire enough energy to support offspring development? What adaptations exist to maximize both infant and maternal survival and what evolutionary trade-offs does this species encounter?

1.4.1 Life History and the Environment

Classically, there are two strategies animals follow for how to accumulate enough energy for reproduction: income breeding and capital breeding (Drent and Daan 1980, Stearns 1992). Income breeding is a reproductive strategy in which females take advantage of predictable seasonal habitats and time births just prior to or during periods of food abundance (Stearns 1992). This is potentially a risky strategy, though, as there is no guarantee that enough food will be available at the required time to meet the added energetic costs, and many income breeders have high rates of infant mortality (Brockman and van Schaik 2005). Hummingbirds, shrews, and roe deer are good examples of income

breeders, as their metabolism precludes them from storing enough energy (Stearns 1989, Andersen et al. 2000, Liu et al. 2003). Species that are larger and take a longer time to develop, or exist in a less-predictable habitat, must use an alternative strategy known as capital breeding, where a mother must maximize her energetic condition prior to conception. This reduces the risk of losing her infant due to a lack of available food resources as she can use her own body fat as an energy source (Emery Thompson 2013b). Phocid seals exemplify this strategy, as 97% of their energy expended during lactation is derived from body fat stores (Bowen et al. 2001). Bighorn sheep are another example of capital breeders, where the reproductive success of a mother is dependent on her body condition going into lactation (Festa-Bianchet 1998, Festa-Bianchet et al. 1998). In highly seasonal habitats, many primate species rely on predictable fluctuations in food availability to subsidize the added energetic costs of reproduction (Brockman and van Schaik 2005, Jones 2011). In reality, because of the extended nature of primate life histories, most primates do not fall explicitly on a pole of the income-capital breeding spectrum and instead utilize varying degrees of both strategies to ensure reproductive success (Emery Thompson 2013a). Female chimpanzees potentially use their condition as a cue they can sustain the costs of gestation and reproduction, and a better condition can act as an energetic buffer during early reproduction (Knott 2001, Ellison 2003, Emery Thompson 2013b). Humans, on the other hand, have shortened lactation periods, increase caloric intake significantly during lactation to support milk production, and rely heavily on post-lactation provisioning of high-calorie food items to infants (Goldberg et al. 1991, Kaplan et al. 2000, van Noordwijk et al. 2013a).

1.4.2 Life History and Energetics

In mammals, lactation is usually the most energetically expensive stage of reproduction and mothers have an increase in energy requirements of 25% to over 150%, depending on the species (Gittleman and Thompson 1988, van Noordwijk et al. 2013b). Individuals that experience an increase in energy intake over time may have shorter reproductive intervals over the course of one's life (Borries et al. 2011, Emery Thompson et al. 2016). This is because an evolutionary tradeoff exists between increased reproductive output and increased parental investment, both of which are viable strategies for increasing overall fitness (Clutton-Brock et al. 1989). How a mother orangutan responds to environmental energy availability across lactation is not yet known, and is an especially interesting question because orangutans exist in unpredictable, marginal environments compared to other apes. In fact, little research has investigated how a mother ape adjusts her foraging strategy to minimize the cost of reproduction and increase her fitness. Several studies have examined variation in chimpanzee activity budget during different reproductive states (Matsumoto-Oda and Oda 1999, 2001, Murray et al. 2009), but these grouped all lactating females into the same category and did not incorporate any energetic data. Human mothers potentially reduce their total energy expenditure four weeks postpartum by reducing activity levels (Goldberg et al. 1991), but these data are based on women in developed countries and it was noted the energy-conserving strategies by women varied extensively.

1.5 Questions and Hypotheses

The main goal of this study is to examine the behavioral and physiological strategies that mother orangutans use to maintain body condition and therefore maximize fitness across periods of infant development, with these three objectives: to determine 1) if a mother modifies her daily activity, dietary composition, and nutritional intake throughout infant development, 2) how the energetic condition of a mother varies across infant development, and 3) how a mother who lactates across multiple years maintains homeostasis in a relatively marginal and variable energetic environment.

In Chapter 2, I explore mother orangutan behavior by investigating 1) if there are key periods during infant development when a mother changes her activity pattern, 2) whether these periods are driven by infant age, preferred food availability (FAI), or both, and 3) if there is an impact on food item selection during these periods. Specifically, I hypothesize that a mother's activity budget, daily path length, length of active period, and percent food items in the diet vary significantly with the age of a mother's infant and the availability of fruit in the habitat.

Chapter 3 investigates the nutritional composition of a mother orangutan's diet. I ask if there is variation in a mother's consumption of macronutrients across infant development and hypothesize that a mother's caloric intake, macronutritional intake, and macronutrient ratio (available protein to non-protein energy) vary significantly with infant age across fruiting periods.

To conclude, in Chapter 4 I bring together multiple forms of noninvasive physiological evidence to understand what the critical energetic periods are for lactating wild mother orangutans. Specifically, I hypothesize that a mother's energetic status, as

measured through ketone body excretion, urinary cortisol, urinary C-peptide, and urea, vary significantly with the availability of fruit in the environment, the age of her infant, and her ingested calories.

1.6 Methods Overview

Since orangutans have such long periods of lactation and resulting interbirth intervals, it is not feasible to observe multiple mother orangutans continuously from an infant's conception to dispersal within the time frame of a dissertation. This project is set up as a cross-sectional study to account for the extended timing of reproductive events in orangutans and utilizes three main methodologies: behavioral observations, macronutrient analysis of food items, and physiological urinary analyses.

1.6.1 Tuanan Research Station

This project took place at Tuanan Research Station in Central Kalimantan, Borneo, Indonesia (02° 09'06''S; 114° 26'26''E; Figures 1.1,1.2). Tuanan is located in the Mawas Conservation Area, an area with one of the world's largest remaining wild orangutan populations at approximately 3,500 individuals (Vogel, personal comm.). Tuanan, established in 2002 by a collaborative team of researchers from Universitas Nasional Jakarta, Bornean Orangutan Survival Foundation, and the University of Zurich, is an internationally-recognized research site for wild orangutan research. Researchers at Tuanan have continuously collected behavioral data on orangutans since July 2003. To date, there are over 125 genetically identified individuals at Tuanan, including ten habituated mother-infant pairs spanning every age range used in this project (Desy, Inul,

Jinak, Juni, Kerry, Kondor, Mindy, Pinky, Sidony, Sumi), making the site ideal for a study of this nature. In addition, since 2003, researchers at Tuanan have collected phenology data on fruiting, flowering, and flushing patterns of 2,400 trees in phenology plots. These data are used to quantify the percentage of fruiting trees (FAI) in the habitat on a monthly basis (Figure 1.3). In 2005, my advisor started a nutritional database that includes the macronutrients of over 200 known orangutan foods consumed in Tuanan.

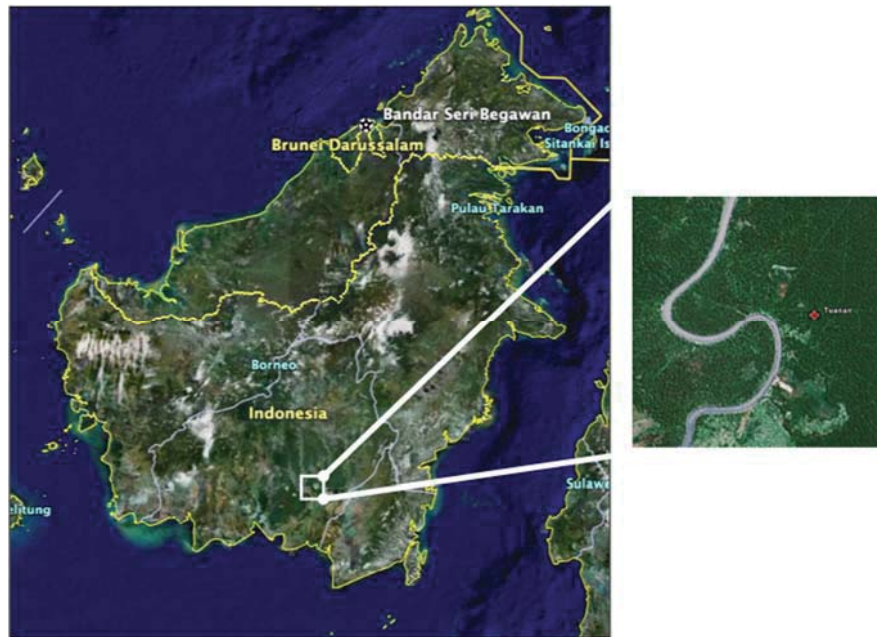


Figure 1.1: *Location of Tuanan Research Station*

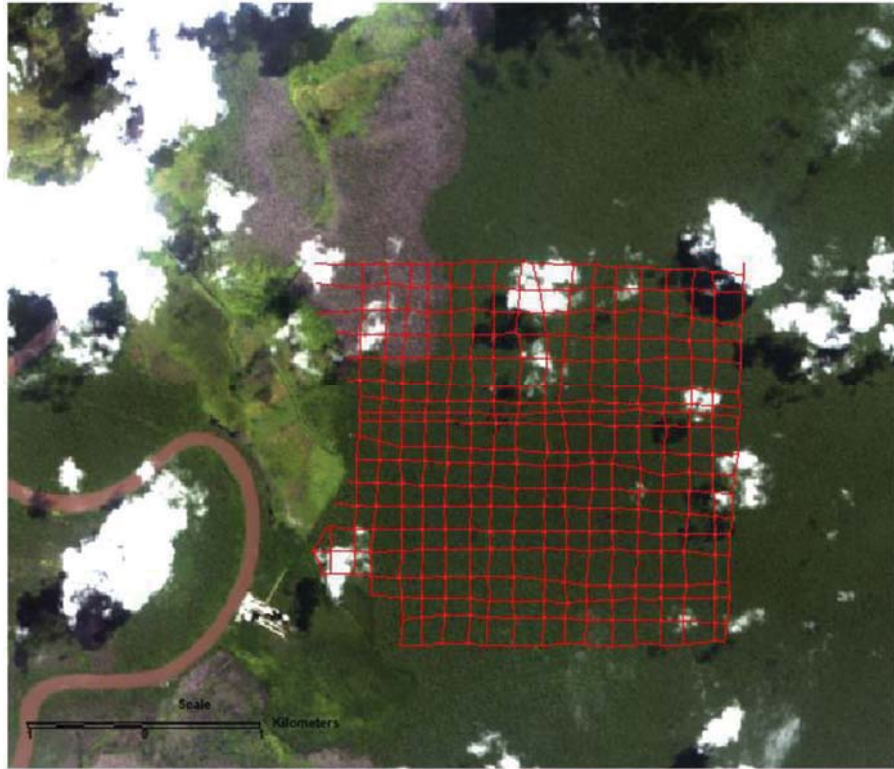


Figure 1.2: *Trail system of Tuanan Research Station (from Alavi, 2018)*

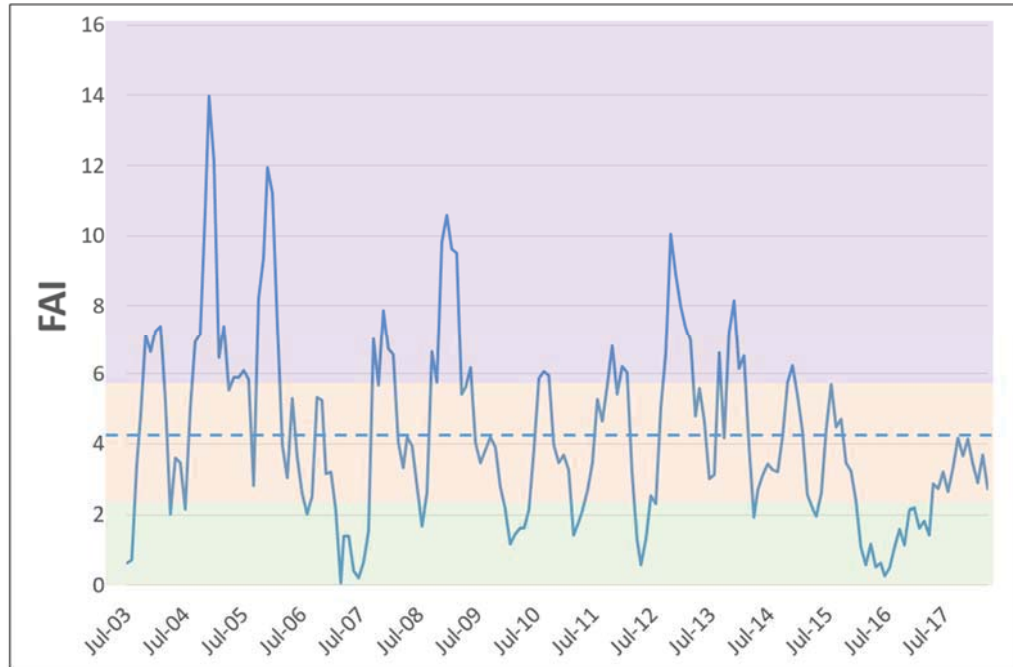


Figure 1.3: Fruit Availability Index fluctuations at Tuanan Orangutan Research Station between July 2003 and March 2018. The green region is the 1st quartile, the orange region is the 2nd and 3rd quartiles, and the purple region is the 4th quartile. The dashed line is the median fruit availability value (4.29%).

1.6.2 Behavioral Observations

In addition to using the long-term behavioral database from Tuanan, I conducted nest-to-nest focal follows on habituated adult females. Protocols from the Orang-utan Data Collection Standardization were used for focal behavioral observation (www.aim.uzh.ch/orangutannetwork; van Noordwijk, 2012). For each follow, I recorded individual name, age class, focal activity, height from ground, and associations with other individuals including distance between them in two-minute intervals. If the focal activity recorded was feeding, then these additional variables were recorded: species of food, food type and part, food maturity, and time feeding per item (feeding rate). Feeding rates

were recorded throughout the duration of a single feeding bout and then averaged for a mean feeding rate for that food patch (Vogel et al. 2015). The specific food types identified were: fruit, young leaves, mature leaves, woody pith, herbaceous pith, flowers, cambium, invertebrates, honey, fungi, vertebrates, soil, and bark. If any other food items are ingested, they will be noted separately. TORP has periodically had a botanist from LIPI Bogor Herbarium come to Tuanan to identify plant species, along with help from Pak Nadi, Pak Rhamatd, Serge Wich, and Nicole Zweifel. The long-term project assistants are familiar with the plant species in the study area and assisted with identification of all unknown food items. New food items were collected and a specimen made for identification at the LIPI Bogor Herbarium.

1.6.3 Macronutrient Collection, Storage, and Analysis

Individual food items, after being judged for close similarity in size and maturation as to those eaten by orangutans, were collected from either the ground or tree from which an orangutan has been observed to feed (Knott 1998). At minimum three samples from each species at specific maturation stages were averaged to account for variation, since it is not possible or practical to sample from every individual tree of a given species at the field site. Samples were brought back to the station and processed as in Vogel et al. (2015, 2017). Samples were dried at 40°C in a kerosene oven until they maintained a constant weight. Dried samples were then sealed, stored with silica gel, and sent to the Laboratorium Pengujian Nutrisi, LIPI-Bogor, Indonesia for nutritional analysis of crude protein, NDF, ash, and lipids under the supervision of Dr. Wartika R. Farida following the methods in Vogel et al. (2015).

1.6.4 Urinary Collection, Storage, and Analysis

Urine was collected from the first void in the morning during focal follows. Either of two methods were employed to collect the urine: 1) spreading a clean plastic sheet beneath a urinating animal or catching the urine in a plastic bag on a stick, or 2) collecting the urine from forest vegetation (Knott 1998). Samples were then split with 2-3 samples of 200µl aliquoted onto filter paper, which were stored in a sealable plastic bag in an airtight container with silica gel, and 4-5 samples of 500ul frozen at -20°C in a solar freezer. Each sample was labeled with time, date, and individual. If the identity of the individual was unknown, the sex, age category, and identifying characteristics were marked. All urine samples were then transported back to the United States under the same storage conditions for laboratory analysis at Rutgers University, including urinary C-peptide and cortisol (see assay procedures below).

Ketone bodies can be quantified in the field using urinalysis strips (Chemstrip 10 UA, Roche Diagnostics) made for humans which have been shown to detect ketones in orangutans (Knott 1998). Ketone bodies were measured twice: once immediately after sample collection while still in the forest, and a second time after returning to the field station laboratory. To use urinalysis strips, 100µl of urine is pipetted onto the strip, and the result is compared with a corresponding color index. The measurement of ketone bodies follows a categorical valuing system: negative, positive, and double positive. This method has been validated in the laboratory with orangutan urine (Naumenko et al. 2016).

1.6.5 Urinary Assay Procedures

For all assays, both forms of samples were transported back to Rutgers University for analysis in Dr. Erin Vogel's Laboratory for Primate Dietary Ecology and Physiology. Collection and export permits were obtained with the assistance of our Indonesian counterpart (UNAS).

Urinary C-peptide of insulin was assayed using a commercial radioimmunoassay kit designed for analysis with urine (EMD Millipore Corporation, St. Charles, Missouri). For the complete procedure, please refer to the Millipore Human C-peptide RIA protocol, which has been validated on orangutan urine (<http://www.emdmillipore.com/US/en/product/Human-C-Peptide-RIA>, MM_NF-HCP-20K; Emery Thompson and Knott, 2008). Cortisol was assayed using a commercially available enzyme-linked immunoassay kit designed for use with urine, among other substances (Arbor Assays, Ann Arbor, Michigan; <http://www.arborassays.com/product/k003-h-cortisol-eia-kit/>). Dr. Vogel and I have validated this kit for use on orangutan urine. To account for variation in urine density, cortisol and UCP should be standardized over a substance that is not affected by muscle mass (Emery Thompson et al. 2012b). Specific gravity is an easy measure that fits this profile (Miller et al. 2004). Specific gravity of urine was measured by a handheld refractometer (Atago PAL-10S) that requires 100µl aliquots of urine, and is measured both in the field and at Rutgers after the samples were transported.

1.6.6 Data Analysis

I used Generalized Additive Mixed Models (GAMM) fit using maximum-likelihood estimation to conduct a cross-sectional analysis on the relationship between the independent variable of infant age and the dependent variables of behavior (feeding, moving, resting, social), food species-item-ripeness combinations, daily caloric intake, nutrient balance (protein, fiber, carbohydrates, lipids), ketone bodies, urinary C-peptide, urea, and cortisol. Because ecological fluctuations may confound these results, all analyses include fruit availability (FAI) as a fixed effect and individual ID as a random effect.

1.6.7 Geometric Framework

I used the Geometric Framework (GF) to analyze if mother orangutans vary the balance of nutrients in their diet throughout different stages of infant development. First, the mean daily nutritional intake for a mother-infant is calculated using the combined behavioral and nutritional data. Then, by plotting two nutrients or sources of energy on each axis, the dietary information for that focal follow with an infant within a specific infant age category is represented as a Cartesian point. Using the created point in space, a line is created from the origin through the point to create a nutritional rail. The slope of the nutritional rail represents the balance between the two or more nutritional attributes being compared. These data were then averaged to calculate a nutritional rail for each mother-infant age group, and GLMMs and GAMMS were used to compare differences and thus show differences in preference between each mother-infant age group if they existed (Rothman et al. 2011, Johnson et al. 2013).

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Chapter 2. The influence of fruit availability and infant age on maternal behavior throughout lactation in wild Bornean orangutans (*Pongo pygmaeus wurmbii*)

2.1. Introduction

For female mammals, lactation is one of the most energetically costly periods, comprising 75-80% of total reproductive energetic costs (Oftedal 1985). During lactation alone, mammals potentially increase caloric intake by over 65% (Gittleman and Thompson 1988), though this is lower for species with extended life histories like primates (van Noordwijk et al. 2013b). Still, the fitness costs associated with lactation far outweigh the costs associated with gestation (Clutton-Brock et al. 1989). Supporting an infant is an inherently taxing activity: in addition to lactation infant care potentially requires protection, provisioning, and carrying (Koenig et al. 1997, Isler and van Schaik 2012). In many species of mammals, mothers must also cope with unpredictable environments that present novel challenges not normally faced by non-mothers, such as infant-specific predators, locating solid foods that can be processed by infants, and periods of inadequate food availability (Kinsley et al. 2008, Schuppli et al. 2016). These factors, among others, push a mother to vary her behavior to ensure the survival of both herself and her offspring, maximizing fitness.

Primate mothers differ in behavioral strategies used to maintain nutritional homeostasis across lactation, including varying levels of activity and dietary items, but this will depend on factors such as infant transportation costs, feasibility of increasing intake, and the length of the lactational period (Dias et al. 2011). Classically, 1) energy

maximization, or increasing total caloric intake, and 2) time minimization, or adjusting activity for reduced energetic expenditure, are potential strategies mammals use to compensate for the added burden of infant care (Schoener 1969, Hixon 1982). These strategies are not mutually exclusive and there are multiple ways to achieve the goals of each. Additionally, we now know that energy is not the sole driver of food selection and individual nutrients play important roles in diet composition (Simpson et al. 1993, Felton et al. 2009a). Increasing nutritional intake can be accomplished through consuming greater amounts of food by: 1) increasing time spent feeding, 2) increasing intake rate either by selecting denser patches or eating faster, or 3) consuming higher quality foods. Compared to cycling and pregnant females, lactating white-faced capuchins (*Cebus capucinus*) increase the amount of food items consumed per unit time, consequently leading to greater energy intake per hour, which frees up time for resting (McCabe and Fedigan 2007, Webb 2017). Hence, they utilize a strategy focused around an increase in quantity of food eaten while altering their activity budget away from time spent foraging. Squirrel monkeys (*Saimiri collinsi*), on the other hand, increase the amount of time they spend foraging while lactating, including the time spent traveling to food sources, in a trade off with time spent resting (Ruivo et al. 2017). Chimpanzee mothers (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania combine two strategies to maximize their nutritional intake (Matsumoto-Oda and Oda 2001, Murray et al. 2009). Lactating mothers both increase the amount of ripe fruit in their diet (higher quality items) and their time spent feeding compared to females in other reproductive states. Instead of increasing nutritional intake, wild siamangs (*Symphalangus syndactylus*) feed significantly less while lactating compared to non-lactating individuals, adjusting their

daily activity to reduce energetic expenditure and fitting the time minimizer strategy (Lappan 2009). Instead of feeding, individuals spend more time with non-lactational care, such as infant carrying, which in turn potentially increases energy expenditure, limits the mother's ability to forage efficiently, and therefore increase the net cost of moving for the purpose of foraging. Humans also reduce their activity levels significantly in the first two months of lactation, increasing their resting time outside of being stationary for milk transfer (Goldberg et al. 1991).

Lactation is not a static state, and the relative quality and quantity of milk synthesized varies depending on resource access, maternal condition, an individual's ability to mobilize body stores, and behavioral interactions between a mother-infant pair (Hinde and Milligan 2011). Therefore, depending on the length of lactation period, a mother potentially utilizes multiple strategies across infant development to support her and her infant's combined needs. Black howler monkeys (*Alouatta pigra*) are a prime example of this. In the first two thirds of her lactation period, a mother will feed more across a broader diet, actively forage across a larger spatial range, and overall rest less than during the final trimester (Dias et al. 2011). She then reduces her foraging activities and increases her resting during the final third of the lactation period. Geladas (*Theropithecus gelada*) show a similar pattern, increasing their feeding time and reducing the amount they rest during the early stages of lactation (Dunbar and Dunbar 1988). Additionally, the threat of infanticide is highest for mothers with infants under one year old (Palombit 2003), and mothers in species such as the chacma baboon (*Papio hamadryas ursinus*) sacrifice nutritional intake and potentially body condition for

increased amounts of resting and vigilance against conspecific individuals in this time (Barrett et al. 2006).

Mother orangutans exhibit multiyear lactation and have the longest lactational period of any primate, with infants nursing for up to eight years spanning multiple unpredictable fruiting cycles (van Noordwijk et al. 2013b, Smith et al. 2017). Infants only start feeding on a non-trivial amount of self-collected solid food early in their second year (van Noordwijk et al. 2013b), and primarily rely on their mothers for traveling long distances for at least two years (Van Noordwijk and Van Schaik 2005, van Noordwijk et al. 2009). Therefore, during lactation the burden on a mother varies extensively both as her infant ages and as the magnitude at which preferred food is available changes unpredictably. Yet, little is known about how mother orangutans modulate their behavior to buffer from these sources of variation across years. Van Noordwijk et al. (2013) described the average daily time budgets of mother orangutans that included both active (day) and inactive (night) periods while exploring maternal investment throughout multiyear lactation. Using linear mixed models, they found that fruit availability, not infant age, was the main determinant for variation in a mother's activity and diet. Still, we don't know if there are critical periods during infant development that yield high costs for a mother or if a mother alters her behavior depending on how much fruit is available. Since orangutans have such long lactation periods that span multiple periods of fruit availability, it is possible they utilize different strategies to survive, including foraging on different food items and altering their daily activity levels.

Here, we explore mother orangutan behavior by investigating 1) if there are key periods during infant development when a mother changes her activity pattern, 2)

whether these periods are driven by infant age, preferred food availability, or both, and 3) if there is an impact on food item selection during these periods. Specifically, we test if a mother's activity budget, daily path length, length of active period, and percent food items in the diet vary significantly with the age of a mother's infant and the availability of fruit in the habitat. We predict that 1) during periods with high fruit availability, mothers, regardless of their infant's age, will seek to maximize nutritional intake due to the greater presence of preferred high quality food items by following patterns seen generally in Bornean orangutans (Harrison et al. 2010, Vogel et al. 2017): increasing their active period, daily path length, time moving, and time feeding to feed more on ripe fruit, while reducing their time resting, 2) during periods of low fruit availability, mothers will seek to conserve energy when they have young, costly infants by reducing their active period, daily path length, and time moving, increasing their time resting and time feeding overall, while foraging more on non-fruit foods, and 3) during medium periods of fruit availability, mothers will attempt to match their behavior during periods of high fruit availability but will not always succeed.

2.2 Methods

2.2.1 Study site and individuals

Data collection took place at Tuanan Orangutan Research Station (Tuanan; 2°09' S and 114°26' E) along the Kapuas Murung River in Central Kalimantan, Borneo, Indonesia. Tuanan is located in the Mawas Conservation Area, an area 3,090km² in size (van Schaik et al. 2005) and containing one of the world's largest remaining wild orangutan populations at approximately 3,500 individuals (Vogel, personal comm.).

Tuanan, established in 2002, is an internationally-recognized research site for wild orangutan research (Wich et al. 2008, Husson et al. 2009). Researchers at Tuanan have continuously collected behavioral data on orangutans since July 2003. To date, there are over 125 genetically identified individuals at Tuanan, including ten habituated mother-infant pairs spanning every age range. Additionally, researchers at Tuanan have collected monthly phenology data since 2003 on fruiting, flowering, and flushing patterns of 2,400 trees in 2.3ha of phenology plots (Vogel et al. 2015). These data are used to calculate the fruit availability index (FAI) in the habitat, which is the percentage of trees fruiting at a given time. While Tuanan does experience an annual high and low fruiting season, researchers still consider the fruiting cycle unpredictable because there is no known inter-annual fruiting cycle for many plant species and the level at which fruiting fluctuates varies drastically from year-to-year (Figure 2.1).

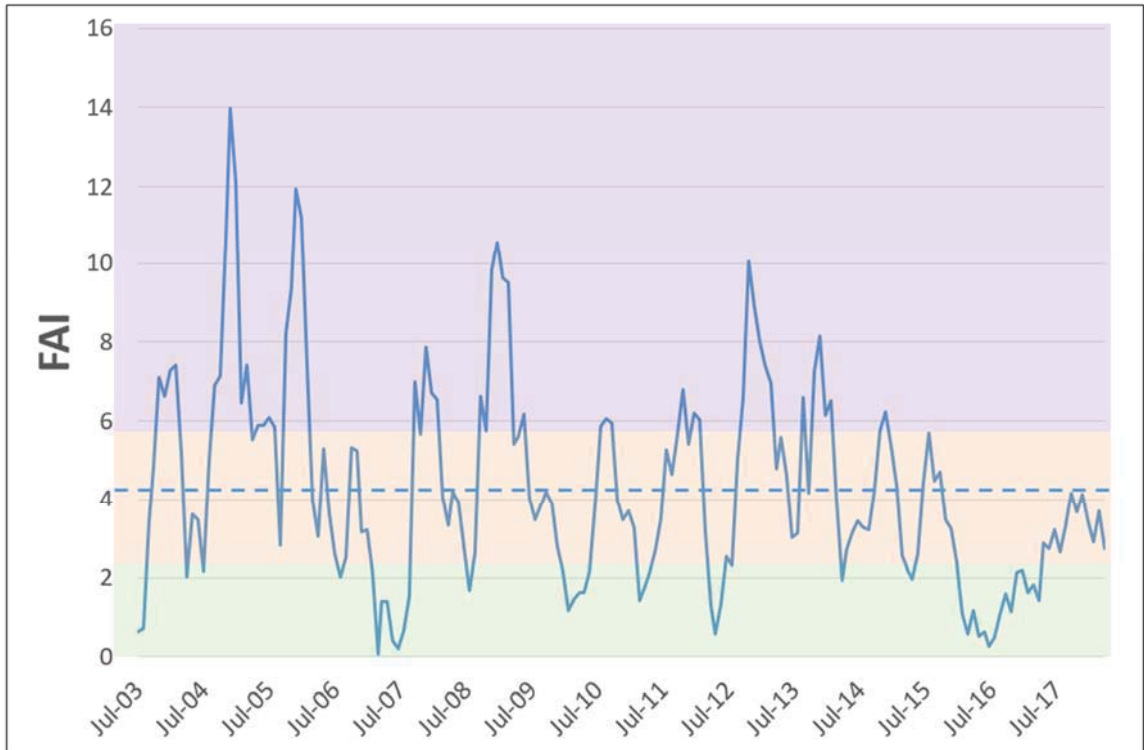


Figure 2.1: Fruit Availability Index fluctuations at Tuanan Orangutan Research Station between July 2003 and March 2018. The green region is the 1st quartile, the orange region is the 2nd and 3rd quartiles, and the purple region is the 4th quartile. The dashed line is the median fruit availability value (4.29%).

2.2.2 Data Collection and Preparation

For this project, we used behavioral data collected on ten lactating females between July 2003 - March 2018 and ranging data were collected on seven of the ten lactating females between July 2003 – July 2012 following protocols from the Orangutan Data Collection Standardization

(<https://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html>; van Noordwijk et al.

2013). A female was assumed to be lactating if she had an infant younger than an estimated age of eight, in accordance with what we know of orangutan lactation (van

Noordwijk et al. 2013b, Smith et al. 2017). Only complete daily follows where the observer was with the orangutan from their morning nest to their night nest were used in the analyses. During each follow, individual name, age class, focal activity, height from ground, and associations with other individuals including distance between them were recorded in two-minute intervals.

2.2.3 Activity Budgets

The focal activities used for this study were feeding, resting, and moving. Social behavior is also collected at Tuanan, but comprised of an average of only 1.39 minutes per day ($\sigma = 3.67$) and was consequently excluded from the study. Multiple follows had periods of time where the observer was not able to detect what activity the focal individual was conducting. To account for this, we excluded any nest-to-nest follows that had greater than 5% unknown activity. Focal activity and length of active period analyses were based on 20,580 hours of observational data ($N = 1,914$ follows; Table 2.1). The average number of follows per month for this study was 11.67 ($\sigma = 7.53$), and no follow was included when it was the only follow in a month, unless it was part of a three day minimum follow period.

To estimate activity budgets, we calculated the minutes per day spent performing specific focal activities. The length of active period for a follow is the amount of time between when an orangutan leaves her morning nest and enters her night nest.

Table 2.1: Number of nest-to-nest follows across infant ages and fruit availability for behavioral data.

Infant Age	Fruit Availability							
	Activity Budget				Daily Path Length			
	Total	High	Medium	Low	Total	High	Medium	Low
0-6 months	269	29	121	119	159	25	65	69
6-12 months	155	10	114	31	92	12	52	28
12-18 months	150	24	74	52	90	23	32	35
18-24 months	204	41	72	91	132	33	47	52
24-36 months	302	83	132	87	206	74	105	27
36-48 months	289	55	134	100	201	42	88	71
48-60 months	205	20	104	81	129	16	64	49
60+ months	340	54	152	134	203	29	84	90
Grand Total	1914	316	903	695	1212	254	537	421

Daily path length (DPL) was calculated from location data from 13,144 hours of observation (N = 1,224 follows; Table 2.1) using the protocols of Vogel et al. (2017). To summarize, two protocols were used depending on when the focal follow occurred. Between 2003-2006, observers used printed maps of the Tuanan study grid with 50m trail intervals to construct hand-drawn paths of the focal individual using a compass, noting their location every 30 minutes. The completed maps were then digitized, DPL was calculated from the polyline distance, and half hour points were compared with the actual travel routes (Wartmann et al. 2010). Starting in 2007, coordinates were taken every 30 minutes using handheld Garmin GPS units. DPL was then calculated using ArcGIS (ESRI, Redlands, CA). Wartmann (2008) found that these two methods did not significantly differ.

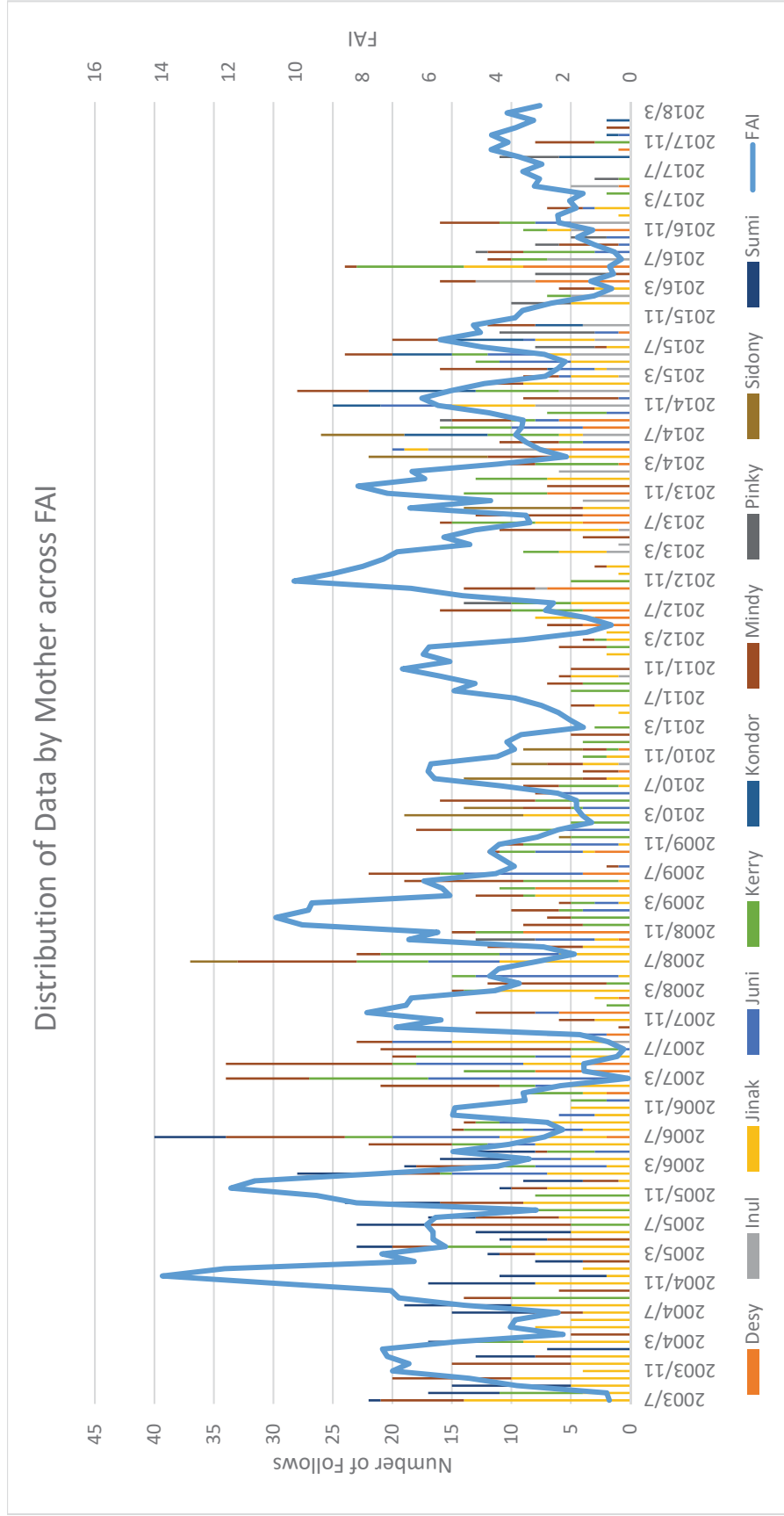


Figure 2.2: Sampled individuals across fruit availability

2.2.4 Feeding Activities

The same data set used to determine activity budget was also used to determine time spent (minutes) eating specific food types. While an orangutan was feeding, we recorded type of food eaten, the stage of ripeness, the length of the feeding bout. The types of food recorded were bark (cambium), pith, flowers, ripe fruit, half-ripe fruit, unripe fruit, insects, mature leaves, young leaves, vegetation (leafy lianas and other vegetative matter), and a category of food items named other (e.g., rare instances of honey consumption). Additionally, we also grouped together mature fruit, half-ripe fruit, and unripe fruit in a separate category called “total fruit.” We did the same for leaves, grouping together mature leaves, young leaves, and vegetation into a category called “total leaves.” In certain circumstances we were not able to accurately view what a food item was and therefore recorded the type as “unknown”.

2.2.5 Statistical Analyses

To analyze the relationship between the dependent variables of a mother’s activity budget, daily path length, length of active period, and time spent consuming food items, and the predictor variables of youngest infant age (in years) and FAI, we constructed generalized additive mixed models (GAMMs) using the *gamm4* package in R statistical software (Wood and Scheipl 2017). GAMMs are semi-parametric extensions of generalized linear mixed models and have several key advantages over generalized linear mixed models when analyzing data sets such as long term behavioral observations (Vogel et al. 2017) and proportional data (Fewster et al. 2000, Polansky and Robbins 2013). First, they do not assume the data fit a specific distribution and instead fit smoothing

terms using penalized regression splines. Second, inference is based on the produced smoothing functions and allow us to interpret specific points where the data vary significantly, instead of determining an overall linear relationship. Each model contained the specified dependent variable, all predictor variables with spline smoothers, the interaction between infant age and FAI using a tensor product smooth, and orangutan ID in a fully maximal random effects structure (random slopes and random intercepts) to prevent pseudo-replication across individual follow days (Harrison et al. 2009). Models were fit using the Gaussian family with an identity link, and knots were selected to be spaced evenly across the axis using the minimal amount possible to avoid overfitting. We included the interaction term to determine if there a mother's activity varied differentially across fruit availability. When the interaction term was significant, we further explored the relationship in two ways: 1) by visualizing the interaction plots, and 2) by constructing GAMMs with a factor-by-variable design. Alongside the dependent variable and FAI was a term splitting infant age by three factors based from FAI quartiles. The three factors used were Low (smallest 25% of FAI values, $FAI < 2.30\%$), Middle (middle 50% of FAI values, $FAI = 2.30\% - 5.90\%$), and High (largest 25% of FAI values, $FAI > 5.90\%$). This design allowed us to see the relationship between the dependent variable and infant age during different periods of fruit availability.

2.3. Results

2.3.1 Activity Budgets

Overall, the average length of a mother's active period was 645.16 minutes ($\sigma = 67.62$) and average daily path length was 764.84m ($\sigma = 392.38$; Table 2.2). Feeding was

the most frequent activity for a mother orangutan, occupying an average of 371.26 minutes per day ($\sigma = 93.57$), followed by resting ($\mu = 154.61$ mins, $\sigma = 77.15$), and moving ($\mu = 80.97$ mins, $\sigma = 41.06$).

Table 2.2: Summary statistics for each activity across fruit availability

Fruit Availability	Activity	
	Length Active Period (mins)	Daily Path Length (m)
High	$\mu = 657.45, \sigma = 59.70$	$\mu = 853.83, \sigma = 393.46$
Medium	$\mu = 646.67, \sigma = 69.63$	$\mu = 831.52, \sigma = 423.08$
Low	$\mu = 637.61, \sigma = 67.50$	$\mu = 626.10, \sigma = 304.07$
Overall	$\mu = 645.16, \sigma = 67.62$	$\mu = 764.84, \sigma = 392.38$
Fruit Availability	Feed (mins)	Move (mins)
High	$\mu = 367.99, \sigma = 88.85$	$\mu = 96.01, \sigma = 40.98$
Medium	$\mu = 369.82, \sigma = 99.21$	$\mu = 84.06, \sigma = 42.74$
Low	$\mu = 374.63, \sigma = 87.96$	$\mu = 70.12, \sigma = 35.74$
Overall	$\mu = 371.26, \sigma = 93.57$	$\mu = 80.97, \sigma = 41.06$
Fruit Availability	Rest (mins)	
High	$\mu = 141.47, \sigma = 69.14$	
Medium	$\mu = 154.02, \sigma = 79.29$	
Low	$\mu = 161.35, \sigma = 77.08$	
Overall	$\mu = 154.61, \sigma = 77.15$	

2.3.1.1 Length Active Period and Daily Path Length

We predicted that a mother's length of active period and daily path length would be longest during high fruiting periods regardless of her infant's age (prediction 1), shortest during low fruit periods with young infants (prediction 2), and that a mother in medium fruit availability would attempt to match her behavior during high fruit availability (prediction 3). Our results support the predictions that a mother's length of active period and path length are significantly longer when there is more fruit in the environment. Because of this result, we included length of active period as a fixed effect

in our behavior models. Our results do not support the predictions that her active period is stable across infant age in periods of high fruit availability or that her path length varies with infant age during low fruiting periods (Table 2.2, 2.3). Instead, a mother's active period is shortest when she has a young infant under one-year-old, regardless of fruiting, but during both low and high fruiting periods her daily path length does not change significantly as her infant ages (Figure 2.3). In support of prediction 3, we see that during medium periods of fruit availability a mother's daily path length does vary significantly depending on the age of her infant. In these circumstances, when a mother has a newborn, her daily path length is similar to that during a high fruiting period, but as her infant approaches two years old it decreases significantly to a length similar to low fruiting periods before rebounding to high-fruiting levels when her infant is around four years old (Figure 2.3).

2.3.1.2 Activities

We predicted that during high fruiting periods, the age of a mother's infant would not impact her behavior significantly, and she would spend more time feeding and moving, while resting less, compared to periods of low fruit availability (prediction 1), and that medium periods of fruit availability would approximate the patterns of high fruiting periods most of the time (prediction 3). Our results support the prediction that a mother's time spent moving increases with fruit availability, but instead show that feeding time is inversely related with fruit availability and has a non-linear relationship with time spent resting (Table 2.3). Overall, a mother rested the most when fruit availability is both at its lowest and highest, but is generally less in-between these two

periods. This result also goes against prediction 3. Additionally, our results show that a mother's time spent moving does indeed vary with infant age, not supporting prediction 1. A mother with an infant under two and a half years old spent less time moving compared to when she has an infant over five years old.

During low fruit availability, we predicted that a mother with a younger infant would spend less time moving and more time both feeding and resting (prediction 2). Our results support the predictions that a mother moves less and rests more with a younger infant (Table 2.3); specifically, we see this variation occur in a mother with an infant around two years old. However, a mother with a two-year-old infant also spent less time feeding than when she has an older infant, going against prediction 2. Interestingly, a mother in moderate fruit availability shows a similar significant pattern in both time moving and time resting, but the level of variation is more reflective of a mother during a high fruit period, providing support for prediction 3.

Table 2.3: GAMM results for activity budget behaviors ($N = 1914$) and daily path length ($N = 1212$).

Model term	Length Activity (mins)			Daily Path Length (m)		
-	<u>p-value</u>	<u>F-stat</u>	<u>df</u>	<u>p-value</u>	<u>F-stat</u>	<u>df</u>
Fruit Availability Index	<0.001	4.917	4.356	<0.0001	10.421	6.430
Infant Age	<0.0001	13.962	7.009	0.002	4.053	4.757
FAI * Infant Age	0.576	0.327	1.180	0.255	1.283	4.085
Active Period	N/A			<0.0001	76.618	3.159
r ²	0.0664			0.328		
AICc	21394.36			17412.77		
Fruit Availability Index	<0.0001	6.614	4.115	<0.0001	12.403	6.468
Infant Age - High FAI	<0.0001	9.652	7.275	0.398	1.451	2.477
Infant Age - Middle FAI	<0.0001	9.798	3.246	<0.0001	7.686	3.876
Infant Age - Low FAI	<0.0001	7.296	7.275	0.252	1.068	1.866
Active Period	N/A			<0.0001	85.637	2.826
r ²	0.0772			0.316		
AICc	21374.91			17417.57		
Model term	Feeding (mins)			Moving (mins)		
-	<u>p-value</u>	<u>F-stat</u>	<u>df</u>	<u>p-value</u>	<u>F-stat</u>	<u>df</u>
Fruit Availability Index	0.008	3.249	5.201	0.154	2.623	2.692
Infant Age	0.452	0.572	3.137	0.056	2.269	4.188
FAI * Infant Age	0.020	2.752	5.421	0.077	1.861	6.188
Active Period	<0.0001	52.130	3.075	<0.0001	54.180	3.484
r ²	0.199			0.237		
AICc	22148.98			19080.08		
Fruit Availability Index	<0.0001	6.031	5.139	<0.001	61.153	1.297
Infant Age - High FAI	0.104	2.560	2.782	0.031	10.680	2.194
Infant Age - Middle FAI	<0.001	6.132	3.836	<0.0001	17.256	3.711
Infant Age - Low FAI	0.048	2.259	3.436	0.029	1.236	1.010
Active Period	<0.0001	53.729	3.008	<0.0001	100.420	3.492
r ²	0.192			0.222		
AICc	22164.44			19093.07		
Model term	Rest (mins)					
-	<u>p-value</u>	<u>F-stat</u>	<u>df</u>			

Fruit Availability Index	0.050	2.070	4.327
Infant Age	0.001	4.267	4.262
FAI * Infant Age	0.853	0.335	4.131
Active Period	0.003	4.561	3.074
r^2	0.0296		
AICc	21818.73		

	p-value	F-stat	df
Fruit Availability Index	0.003	4.303	4.719
Infant Age - High FAI	0.063	2.676	2.446
Infant Age - Middle FAI	0.034	2.546	3.254
Infant Age - Low FAI	0.011	3.036	3.613
Active Period	<0.001	5.276	3.764
r^2	0.0322		
AICc	21817.73		

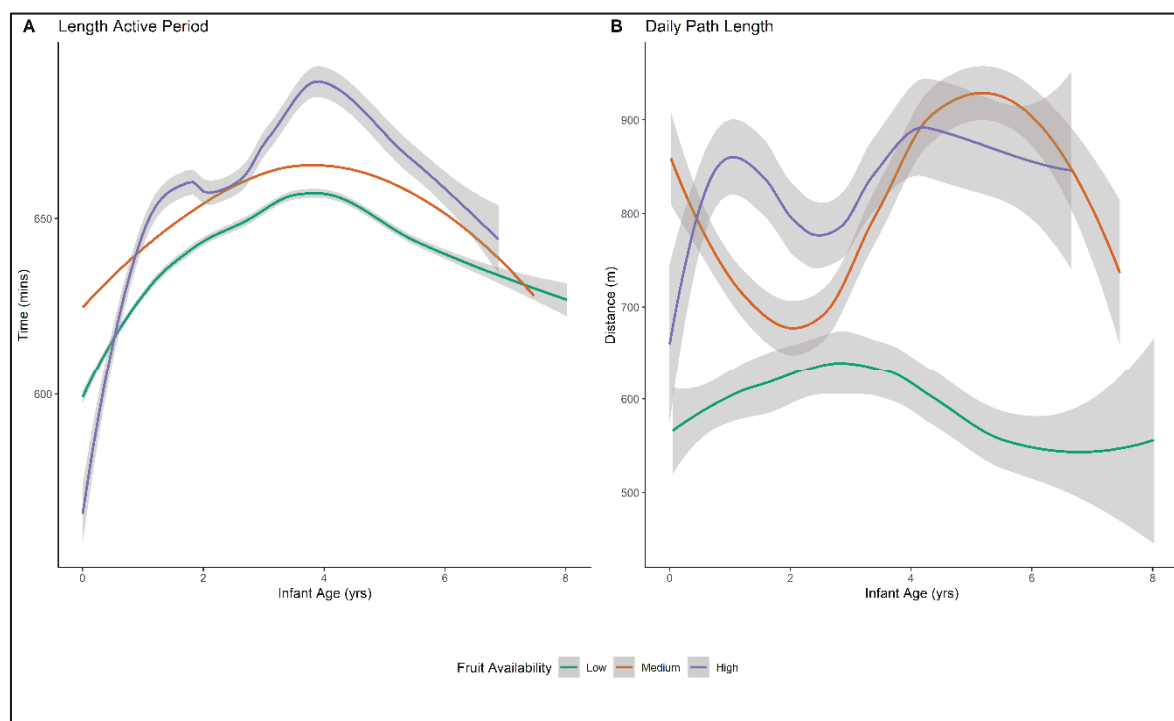


Figure 2.3: Approximate smoothing terms for GAMM outputs across both infant age and fruit availability for a mother's a) length of active period and b) daily path length.

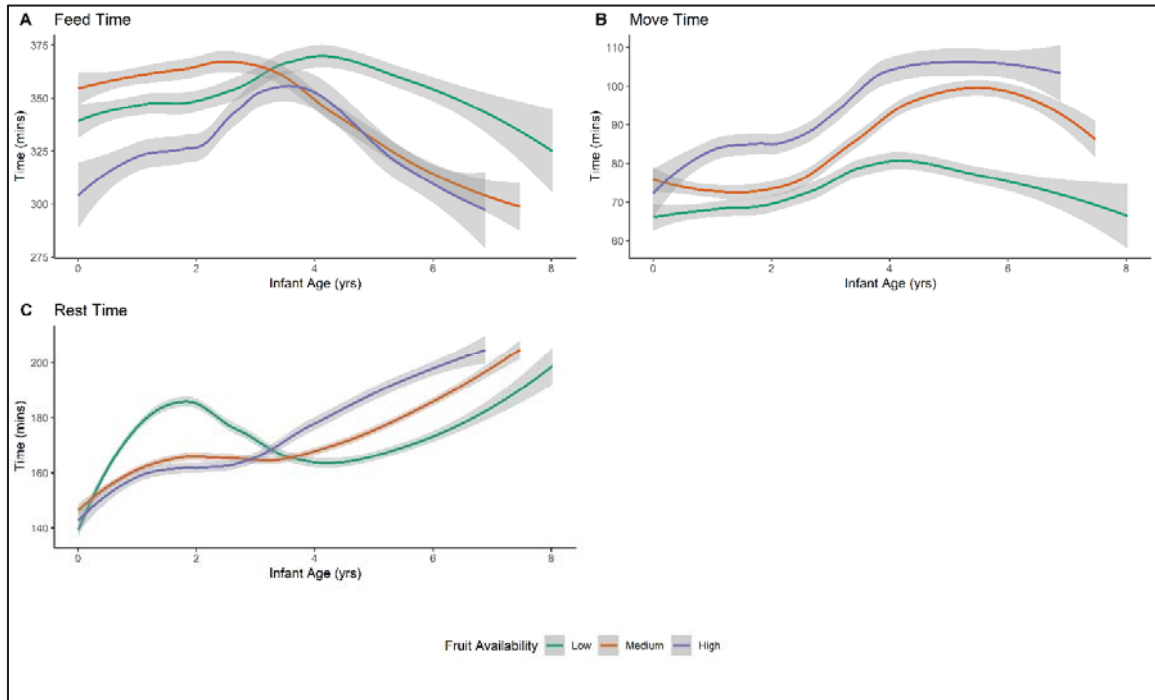


Figure 2.4: Approximate smoothing terms for GAMM outputs across both infant age and fruit availability for a mother's a) time spent feeding, b) time spent moving, and c) time spent resting.

2.3.2 Feeding Activities

In terms of average time spent consuming a food, half-ripe fruit was the most common food item in the diet overall, and the most common item in both medium and low periods of fruit availability (Table 2.4). As would be expected, in high fruiting periods a mother spent the largest amount of time feeding on ripe fruit. Young leaves were also common, with a mother spending the third most amount of time overall consuming them, and were most present in the diet during periods of low fruit availability. A mother spent around 50 minutes consuming flowers during low fruiting

periods, but only 8 minutes during high fruiting periods. Fruit availability significantly impacted a mother's time spent consuming all food items, except for insects (Table 2.5). Since feeding time is significantly correlated with fruit availability, we added feeding time to the model as a fixed effect. Every food item in a mother's diet was positively correlated with feeding time, except for leaves and pith, where feeding time had no effect (Table 2.5).

Table 2.4: Mean time spent foraging on each food item across fruiting periods. Top three food items in each fruiting period in bold.

Food Type	Fruit Availability							
	Overall (mins)		High (mins)		Medium (mins)		Low (mins)	
	mean	sd	mean	sd	mean	sd	mean	sd
Cambium	12.54	33.78	1.62	7.18	5.51	21.68	26.63	46.84
Flowers	39.03	95.67	8.09	24.51	41.77	98.85	49.54	108.16
Ripe Fruit	65.20	105.54	118.18	130.79	65.98	103.67	40.09	84.03
Half-ripe Fruit	129.89	149.24	92.31	139.58	159.18	158.67	108.91	132.79
Unripe Fruit	46.15	85.99	72.89	108.66	40.20	78.32	41.71	81.60
Unknown Fruit	13.88	47.78	30.49	75.85	9.58	38.11	11.92	40.51
Insect	15.76	45.22	17.76	41.22	15.20	46.49	15.57	45.32
Mature Leaves	10.47	32.07	7.46	22.82	10.90	37.10	11.28	28.36
Other	0.18	1.46	0.18	0.87	0.21	1.39	0.15	1.74
Pith	5.76	22.73	2.27	12.77	2.89	12.66	11.08	33.12
Vegetation	15.11	29.60	7.66	14.86	9.75	25.11	25.47	36.40
Young Leaves	55.60	62.98	40.35	47.52	51.71	64.74	67.57	64.75

2.3.2.1 High Fruit Availability

We predicted that a mother would feed on more ripe fruit during periods of high fruit availability, regardless of infant age (prediction 1). We found that as fruit availability increased, a mother spent more time consuming fruit, especially ripe and unripe fruit, supporting prediction 1 (Table 2.5). A mother's time spent consuming half-

ripe fruit peaked around the threshold between medium and high fruit availability, then decreased. Overall, a mother in a high fruit period potentially fed 70 minutes more on ripe fruit and 100 minutes more on total fruit than during a low fruit period. However, our prediction 1 is not supported with regards to the age of a mother's infant. A mother with an infant younger than two years old during high fruiting periods spent significantly more time consuming ripe fruit than a mother with an older infant in the same period (Table 2.5; Figure 2.5). Conversely, a mother's time spent consuming half-ripe fruit increases with infant age during high fruit availability. This results in a mother's net time spent eating fruit overall during high fruiting remaining relatively stable. Outside of time spent consuming ripe and half-ripe fruit, a mother's dietary composition does not vary otherwise with the age of her infant (Table 2.5).

Table 2.5: GAMM results for time spent feeding on different food items across infant age and FAI. Total fruit is the aggregate time of ripe, half-ripe, and unripe fruit. Total leaves is the aggregate time of mature leaves, young leaves, and vegetation.

Model term	Bark (mins)			Flowers (mins)			Pith (mins)		
	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
-									
Fruit Availability Index	<0.0001	23.38	6.07	0.002	4.011	4.35	<0.0001	8.785	4.31
Infant Age	0.517	0.797	3.62	0.458	0.961	3.49	0.051	2.738	3.14
FAI*Infant Age	0.999	0.011	3.83	0.993	0.057	3.91	0.997	0.089	5.98
Feeding Time	0.007	6.972	1.06	<0.0001	15.15	4.33	0.184	1.473	3.56
r ²	0.206			0.0729			0.0869		
AICc	18481.77			22728.31			17270.28		
	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
Fruit Availability Index	<0.0001	64.90	6.19	<0.001	5.142	4.91	<0.0001	21.92	5.63
Infant Age - High FAI	0.6756	0.403	2.15	0.442	0.577	1.09	0.6302	0.429	2.28
Infant Age - Middle FAI	0.3797	1.061	3.44	0.619	0.872	3.11	0.050	3.844	1.00
Infant Age - Low FAI	0.031	3.376	2.23	0.078	1.907	3.42	<0.0001	6.534	4.78
Feeding Time	0.024	3.73	2.01	<0.0001	16.73	4.16	0.225	1.71	2.25
r ²	0.203			0.0777			0.0809		
AICc	18481.26			22717.81			17271.91		
Model term	Ripe Fruit (mins)			Half-ripe Fruit (mins)			Unripe Fruit (mins)		
	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
-									
Fruit Availability Index	0.031	2.266	4.71	<0.0001	12.15	5.11	<0.0001	5.922	6.12
Infant Age	0.215	1.521	3.44	0.014	3.280	3.97	0.899	0.313	3.75
FAI*Infant Age	0.395	1.168	4.06	0.090	1.834	5.48	0.819	0.503	4.48
Feeding Time	0.015	3.375	3.29	<0.0001	8.646	3.72	<0.0001	11.64	4.68
r ²	0.092			0.097			0.104		
AICc	22861.81			24222.89			22284.79		
	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
Fruit Availability Index	<0.001	5.704	4.50	<0.0001	20.55	5.98	<0.0001	7.774	6.13
Infant Age - High FAI	<0.0001	11.19	2.59	<0.0001	13.72	1.95	0.459	0.678	2.47

Infant Age - Middle FAI	0.026	3.558	3.31	0.013	3.202	4.02	0.033	2.823	4.36
Infant Age - Low FAI	0.217	1.570	3.05	0.827	0.056	1.41	0.057	2.093	3.52
Feeding Time	0.004	4.285	3.24	<0.0001	6.921	4.13	<0.0001	12.70	4.49
r ²	0.126			0.091			0.105		
AICc	22820.02			24218.25			22278.94		
Model term	Mature Leaves (mins)			Young Leaves (mins)			Vegetation (mins)		
	p-val	F	df	p-val	F	df	p-val	F	df
Fruit Availability Index	0.191	1.411	4.26	<0.0001	8.859	5.62	<0.0001	10.71	5.21
Infant Age	0.687	0.591	3.68	0.043	2.956	4.25	0.172	1.595	3.89
FAI*Infant Age	0.676	0.690	4.66	0.818	0.464	3.74	0.987	0.089	3.93
Feeding Time	0.776	0.421	3.78	0.266	1.023	3.79	0.383	1.045	4.92
r ²	0.00491			0.0791			0.125		
AICc	18451.52			21077.81			18149.11		
	p-val	F	df	p-val	F	df	p-val	F	df
Fruit Availability Index	0.065	2.303	4.21	<0.0001	11.76	5.83	<0.0001	26.00	5.18
Infant Age - High FAI	0.8139	0.169	2.61	0.69042	0.488	2.43	0.8136	0.302	2.29
Infant Age - Middle FAI	0.160	2.029	3.53	<0.0001	6.758	4.30	0.544	0.559	3.23
Infant Age - Low FAI	0.385	1.064	3.11	0.004	4.686	3.56	0.020	4.087	2.92
Feeding Time	0.640	0.399	1.96	0.291	0.955	3.79	0.462	0.917	4.90
r ²	0.00246			0.0816			0.124		
AICc	18443.96			21067.22			18145.18		
Model term	Total Fruit (mins)			Total Leaves (mins)			Insects (mins)		
	p-val	F	df	p-val	F	df	p-val	F	df
Fruit Availability Index	<0.0001	11.68	6.55	<0.0001	13.66	5.91	0.090	1.679	5.19
Infant Age	0.373	1.172	2.20	0.319	1.294	3.52	0.631	0.540	3.13
FAI*Infant Age	0.789	0.471	4.70	0.904	0.273	4.50	0.926	0.161	3.17
Feeding Time	<0.0001	48.98	5.75	0.579	0.569	3.39	<0.0001	12.97	5.90
r ²	0.282			0.137			0.0863		
AICc	23809.77			21671.92			19813.99		
	p-val	F	df	p-val	F	df	p-val	F	df
Fruit Availability Index	<0.0001	56.07	5.92	<0.0001	24.36	5.29	0.092	1.701	4.76

Infant Age - High									
FAI	0.79134	0.402	2.51	0.648	0.651	2.34	0.190	1.835	2.60
Infant Age -									
Middle FAI	<0.001	6.65	3.04	<0.001	7.500	3.45	0.687	0.463	2.65
Infant Age - Low									
FAI	0.174	2.622	1.60	0.010	3.722	3.10	0.282	1.678	2.77
Feeding Time	<0.0001	49.59	5.52	0.620	0.559	3.83	<0.0001	12.69	5.89
r ²	0.282			0.142			0.0856		
AICc	23793.95			21654.18			19806.66		

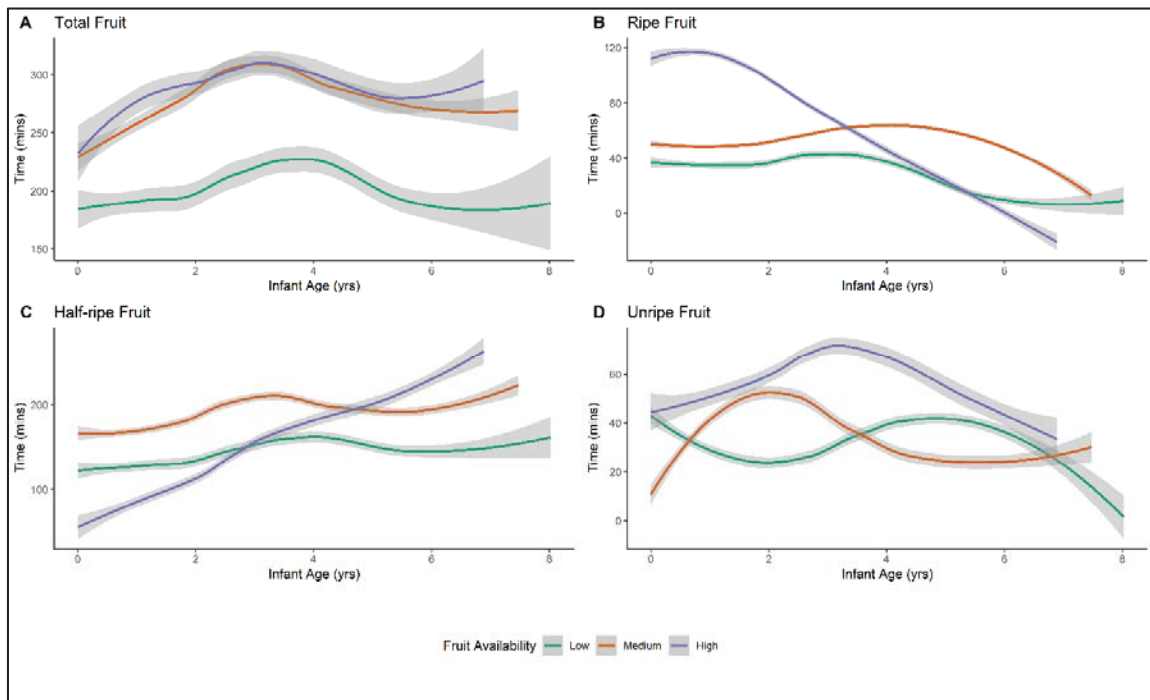


Figure 2.5: Approximate smoothing terms for GAMM outputs across both infant age and periods of fruit availability for a mother's proportion time feeding on a) total fruit, b) ripe fruit, c) half-ripe fruit, and d) unripe fruit.

2.3.2.2 *Low Fruit Availability*

We predicted that during low fruiting periods, a mother with a young infant would feed more on non-fruit items (prediction 2). A mother's time spent feeding on leaves, bark, flowers, and pith decreased as fruit availability increased, supporting prediction 2 (Table 2.5). During low fruit periods, her time spent feeding on vegetation is joint-highest while she has an infant under two years old, her bark consumption is highest while she has an infant under two years old, and her time spent eating pith peaks when she has an infant around two years old (Table 2.5; Figure 2.6, 2.7) is highest while she has a young infant. Additionally, in these periods a mother has a significant spike in time spent consuming leaves when her infant is under two years old, a near-significant spike in time spent feeding on flowers when her infant is around two years old, and no change in her time feeding on fruit items. In general, during a low fruit period a mother with a two-year-old infant spent around 150 minutes more feeding on non-fruit items than a mother during a high fruit period, while spending overall less time feeding. Collectively, these results support prediction 2 and demonstrate that a mother orangutan is feeding more on items other than fruit while she has a young infant in a period of low fruit availability, especially when her infant is around two years old (Table 2.6).

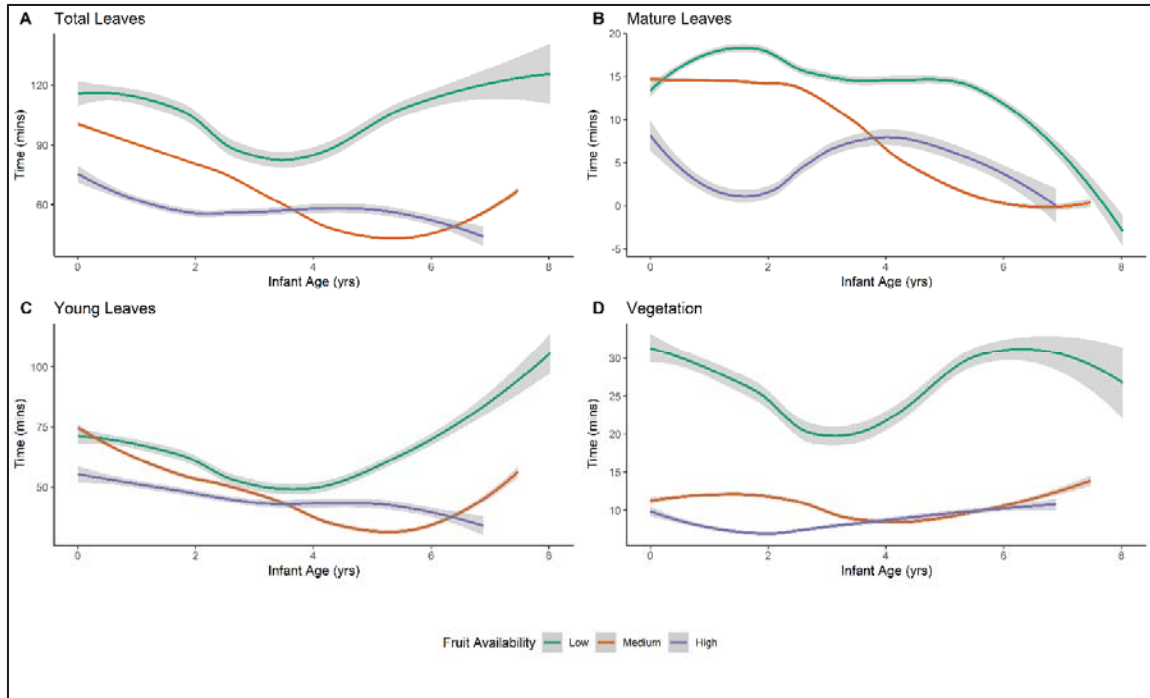


Figure 2.6: Approximate smoothing terms for GAMM outputs across both infant age and periods of fruit availability for a mother's proportion time feeding on a) total leaves, b) mature leaves, c) young leaves, and d) vegetation.

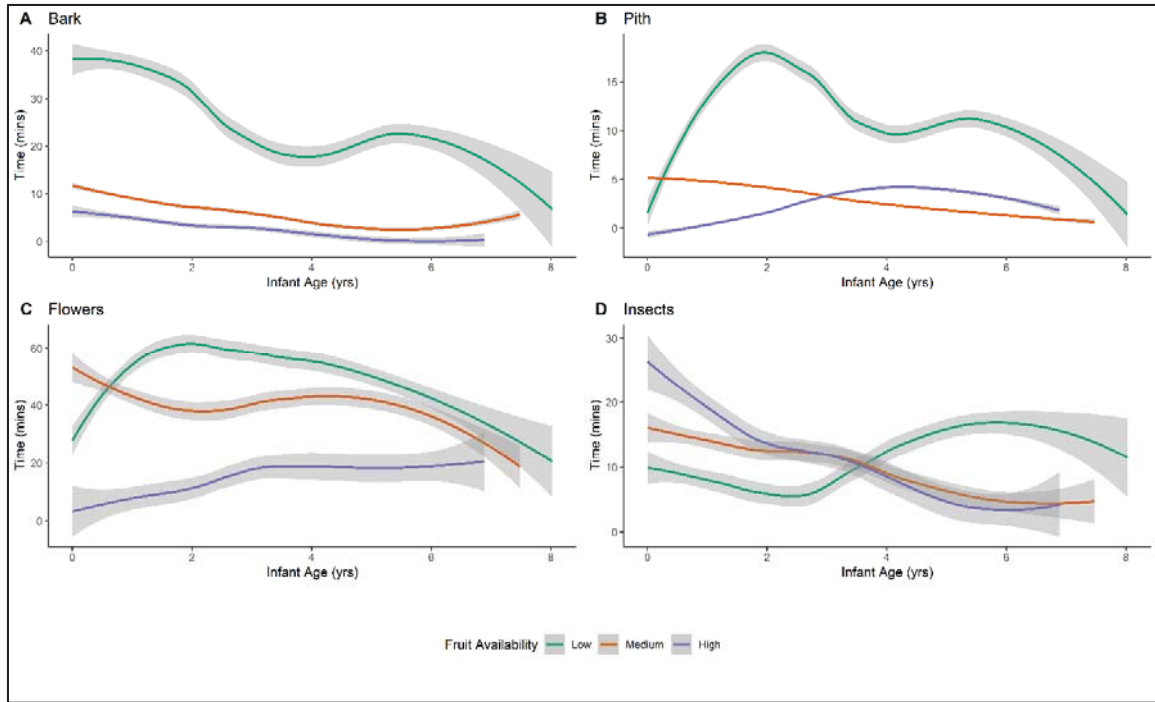


Figure 2.7: Approximate smoothing terms for GAMM outputs across both infant age and periods of fruit availability for a mother's proportion time feeding on a) bark, b) pith, c) flowers, and d) insects.

2.3.2.3 Medium Fruit Availability

We predicted that a mother during medium periods of fruit availability would attempt to feed on a similar diet to a mother in a high fruiting period (prediction 3). We found support for this prediction, as during periods of medium fruit availability a mother's ripe fruit and half-ripe fruit consumption does indeed follow similar patterns as during high fruit availability (Table 2.5; Figure 2.5). However, instead of a spike in ripe fruit consumption when a mother has a young infant around two years old, we instead see an increase in unripe fruit consumption. At this same juncture in fruit availability and infant age, we also see a mother spent significantly more time feeding on leaves,

especially young leaves, compared to when she has an older infant around five years old (Table 2.5; Figure 2.6). Taken together, these results support prediction 3, as mothers are attempting to maintain similar amounts of fruit consumption, but feeding on less-preferred food items when ripe fruit is less available (Table 2.6).

Table 2.6: Summary of results for each combination of fruiting period, activity, and food item.

		Fruiting Period		
		High	Medium	Low
Behavior (estimated range)	Feeding (300 - 370 mins)	-Lower overall -Does not vary with infant age	-Decreases with infants >3yo	-Higher overall -Lower with infants ~2yo
	Resting (140 - 200 mins)	-Does not vary with infant age	-Increases with infants ~3yo	-Higher with infants ~2yo
	Moving (65 - 110 mins)	-Higher overall -Lowest with infants <2yo	-Lowest with infants ~2yo -Highest with infants ~5yo	-Lower overall -Lower with infants ~2yo
	Active Period (580 - 680 mins)	-Longer overall -Plateau with infant ~1.5yo -Shortest with infants <1yo	-Shortest with infants <1yo -Longest with infants ~4yo	-Shorter overall -Shortest with infants <1yo
	Daily Path Length (500m - 1100m)	-Longer overall -Does not vary with infant age	-Lowest with infants ~2yo	-Shorter overall -Does not vary with infant age
Food Item (estimated range)	Total Fruit (175 - 310 mins)	-Higher overall	-Increases between 0-3yo infants -Same as high FAI when infant >3yo	-Lower overall -Does not vary with infant age
	Ripe Fruit (20 - 120 mins)	-Higher overall -Steep peak with infants ~1.5yo, then rapid decline	- Slight increase and stabilization with 3yo infant	-Lower overall -Does not vary with infant age
	Half-ripe Fruit (50 - 225mins)	-Lowest with infants <2yo, then steady rise	-Higher overall -Slight increase after 2yo infant	-Lower overall -Does not vary with infant age
	Unripe Fruit (20 - 700 mins)	-Higher overall -Does not vary with infant age	-Peak with infants ~2yo	-Lower overall -Does not vary with infant age

Total Leaves (50 - 120 mins)	-Lower overall -Does not vary with infant age	-Lowest with infant ~5.5yo	-Higher overall -Nadir with infants ~3yo
Mature Leaves (0 - 20 mins)	-No relationship	-No relationship	-No relationship
Young Leaves (25 - 110 mins)	-Lower overall -Does not vary with infant age	-Lowest with infant ~5.5yo	-Higher overall -Nadir with infants ~3.5yo
Vegetation (0 - 35 mins)	-Lower overall -Does not vary with infant age	-Does not vary with infant age	-Higher overall -Nadir with infants ~3yo
Bark (0 - 40 mins)	-Does not vary with infant age	-Does not vary with infant age	-Higher overall -Highest with young infants
Pith (0 - 20 mins)	-Does not vary with infant age	-Does not vary with infant age	-Higher overall -Peak with infants ~2yo
Flowers (0 - 65 mins)	-Lower overall -Peak with infants ~2yo	-Does not vary with infant age	-Higher overall -Peak with infants ~2yo
Insects (0 - 25 mins)	-Does not vary with infant age	-Does not vary with infant age	-Does not vary with infant age

2.4. Discussion

Our results support all three of our hypotheses and predictions to some degree, showing that mother orangutans vary their behavioral strategy depending on both the availability of fruit in the environment and the age of their infant (summarized in Table 2.6). During high fruiting periods, mothers have the longest active periods and daily path lengths while also increasing their time spent moving. Additionally, they feed more on ripe fruit and less on other items, fitting the model of nutritional maximization and supporting prediction 1. During periods of low fruit availability, mothers rest more and move less, while feeding a similar amount of time on items other than fruit, especially

with infants less than two years old, supporting prediction 2 and fitting the model of time minimization. Where there are moderate levels of fruit availability, mothers with younger infants more closely resemble mothers in low fruiting periods, especially in regarding to time spent feeding, moving, and consuming ripe fruit. As her infant ages, a mother transitions to more closely resemble nutritional maximization. Several key pieces of information from the analyses stand out: 1) the spike in ripe fruit feeding in mothers with young infants followed by a drop-off around two-years-old during high periods of fruit availability, 2) the increase in a mother's moving time starting when she has an infant between three and four years old during both high and medium periods of fruit availability, 3) a mother's increased time spent feeding on non-fruit items like leaves, bark, and pith when she has an infant less than three years old in low fruit periods, and 4) the amount of behavioral and dietary changes in mothers with infants around two years old.

2.4.1 Flexibility Strategies during High Fruit Availability

In high periods of fruit availability, a mother seemingly switches between two strategies for maximizing nutritional intake depending on her infant's age. While she has a younger infant, a mother spends more time feeding on ripe fruit and increases her active period, but not her daily travel. This strategy is similar to those of squirrel monkeys, where mothers sacrifice resting to move to fruiting trees and feed for longer periods of time (Ruivo et al. 2017). Once infants are capable of moving more independently (van Noordwijk et al. 2009) and physically able to process greater numbers of food items (Schuppli et al. 2016), we then see mothers adopt a strategy more similar to chimpanzees

(Murray et al. 2009). When her infant is around two and a half years old, a mother's time moving increases, but her ripe fruit consumption decreases as she spends more time feeding on half-ripe fruit. Still, her overall fruit consumption is stable, potentially meaning she is now able to access preferred food items and/or preferred micronutrient balance more easily. Three-year-old infants at Tuanan can consume approximately 50% of a mother's dietary repertoire, compared to only around 30% when they are two years old (Schuppli et al. 2016), and this 20% of newly-consumable foods by infants may represent the preferred foods of mothers. Future research investigating variation in a mother's macronutrient intake and food item selection will be able to determine if this is indeed the case. Unfortunately, our dataset contains average, not bout-specific, feeding rates so we cannot answer the question if a mother's intake rate increases within a given time, such as seen in capuchins (McCabe and Fedigan 2007). The decrease in a mother's feeding time on ripe fruit seen during high fruit periods may also be a return to normal behavior after an increase in ripe fruit consumption to support the early lactation, as seen in both howler monkeys and geladas (Dunbar and Dunbar 1988, Dias et al. 2011). However, finding an adult female orangutan without an infant in the wild is a rare occurrence (Mitani 1989, van Noordwijk et al. 2013b), and it is therefore extremely difficult to determine baseline levels of activity for wild adult females.

2.4.2 Time Minimization during Low Fruit Availability

Previous studies state that adult female orangutans feed on fruits ca. 70% of the time (Morrogh-Bernard et al., 2009), but our analyses show this is only true during medium and high fruiting periods, when half-ripe and ripe fruit is more widely available.

During periods of low fruit availability, orangutan mothers must rely more on food items other than fruit, as seen by increases in leaf, bark, and pith consumption, especially with two-year-old infants. Collectively, a mother can feed on these items 150 minutes more than during high fruit periods with a similar-aged infant. Leaves, bark, and pith, which take longer amounts of time to process (Schuppli et al. 2016) and digest (Lambert 1998), limit a mother's ability to search for the more preferred food that is available. When combined increased resting time and overall lower time moving, daily path length, and active period, this information supports the idea that mothers do not seek to maximize energy and nutrients. Instead, they reduce their activity levels and expend less energy to compensate for foraging on relatively poorer quality foods. This is opposite of what is found in white-bearded gibbons (*Hylobates albibaris*) at the same field site, who travel farther to acquire unripe fruit and figs during periods of fruit scarcity (Vogel et al. 2009). Interestingly, a similar time minimization strategy is seen in the siamang (*Symphalangus syndactylus*), another Southeast Asian ape, though siamangs are able to offset parental costs by sharing infant-carrying responsibilities (Lappan 2009).

2.4.3 Period of Maximum Maternal Cost

Maternal cost in mammals is defined to include the classic definition of parental investment (time and energy needed for a parent to invest in a specific offspring; Trivers, 1972) along with parental behaviors that overall improve an offspring's chances of survival at the expense of the mother (Clutton-Brock 1991). Regardless of the fruit availability, mother orangutans change their behavior as their infant approaches the age of two. In periods of high fruit availability, a mother moves less, is less active overall,

and starts to reduce her ripe fruit intake when her infant is at this age. In medium fruit periods, a mother has her lowest daily path length with infants around two years old and only begins to shift her behavior to match that of mothers in higher fruit periods once her infant is older. A mother's leaf, bark, and pith consumption is higher overall, and her resting increases while fruit consumption and movement decrease at this stage in low fruit periods. Additionally, during periods of low fruit availability a mother with an infant around two years old spends about 30 minutes less time consuming leaves than with either a younger or older infant, presumably impacting her caloric intake. Taken together, maternal cost is at its highest while a mother has an infant around two years old. After two years old, her infant is more capable of foraging and movement, and less investment is needed from the mother (van Noordwijk et al. 2009). Previous research on various aspects of orangutan social behavior and mother-infant interactions support this concept. As mentioned previously, infants only start consistently feeding on solid food around the age of 12-18 months (van Noordwijk et al. 2013b). As they approach two years old, infants are still in contact with the mother over 80% of the time while moving (van Noordwijk et al. 2009), and infants aren't able to cross tree gaps on their own until they are approximately two and a half years old (Chappell et al. 2015). Dietary competence in infants is still relatively low at two years old (Schuppli et al. 2016) and food sharing initiated by the infant is still common (Jaeggi et al. 2008). Collectively, this demonstrates that a mother orangutan's cost of supporting an infant is greatest when the infant is between one and a half and two years old. Mothers in high fruit periods are restricted in their search for high quality food, and mothers in low fruit periods must minimize expensive activities in order to persist through this period of maximum maternal cost. It

is important to note that throughout the study period there have been periods where a mother has given birth to an infant while her older offspring is still in association, which may last for up to two years longer (van Noordwijk, pers. comm.). While older infants are nearly as competent in locomotion and feeding capabilities as adult orangutans (Jaeggi et al. 2010, Chappell et al. 2015, Schuppli et al. 2016), the presence of an older offspring potentially influences the foraging behavior and decision making of a mother, including increasingly the potential for food competition. However, this social context only adds to the magnitude of costs experienced by a mother with a young infant. Future research using a dataset with higher resolution on social interactions between a mother and infant can help elucidate the impact of an older offspring present on maternal cost.

2.4.4 Conclusions

Our analyses demonstrate that a mother orangutan in a peat swamp forest utilizes different strategies to support herself throughout lactation depending both on her infant's age and how much preferred food is in the environment. In high fruit periods, a mother will switch to a nutritional maximization strategy. Here, she travels more to feed on ripe fruit, as seen by longer active periods and an increase in time spent feeding on ripe fruit. During periods of low fruit availability, however, a mother adopts a time-minimization strategy by conserving as much energy as she can, reducing her activity and utilizing what energy she has to feed on relatively more types of food items. This is especially evident when a mother has an infant just under the age of two. In this period, she spends less time moving, has shorter active periods and path lengths, and increases time spent resting. Even in high fruit periods, a mother exhibits behavioral variation when her infant

is around two years old that imply she is taxed, such as decreasing her time spent moving and an increase in ripe fruit consumption compared to when she has an older infant. This can be thought of as the period of maximum maternal cost. The threshold where a mother changes strategy more than likely depends on finer scale habitat variation, including when specific foods become available, her nutritional needs, and the level of fat reserves currently available to her. The following chapters take a more in-depth look into variation in macronutrient intake and biomarker changes in energetic status by mother orangutans depending on the same independent variables used here: infant age and fruit availability.

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Chapter 3. Variation in macronutrient intake and macronutrient ratios during motherhood in wild Bornean orangutans (*Pongo pygmaeus wurmbii*)

3.1 Introduction

Growth, maintenance, survival, and reproduction are all influenced by an animal's ability to acquire sufficient nutrients nutritional intake (Altmann 1998). When animals forage, they often must choose among foods that are nutritionally imbalanced (Simpson et al. 2004). That is, foods have various ratios of macronutrients that might lead to an intake excess of some nutrients and a deficit of others. The most accessible energy for orangutans and many other primates is found in non-protein nutrients, particularly carbohydrates, which are highest in ripe fruits. While protein is essential for growth, development, and maintenance (Vogel et al. 2012b), energy from protein is less accessible than other macronutrients (Exton 1972), so there exists a tradeoff in food selection between protein-rich foods like young leaves and other more non-protein energy-rich items. Animals are expected to navigate this tradeoff, but are not always successful, in a way that maximizes their fitness (Schoener 1971). Many tropical habitats exhibit seasonality in both ripe fruit and young leaves which influences the foraging strategy and feeding behavior of herbivorous and omnivorous primate species (Janson and Chapman 1999, van Schaik and Pfannes 2005). In the peat-swamp forests of Indonesia, the unpredictable nature of fruiting cycles in both timing and magnitude creates an ever-changing nutritional landscape for preferential frugivores, like orangutans, to navigate (Wich et al. 2011, Vogel et al. 2017).

Multiple studies have compared the macronutrient and energetic intake of various populations and age-sex classes of orangutans (Knott 1998, 2005, Conklin-Brittain et al. 2006, Harrison et al. 2010, Vogel et al. 2015, 2017). Bornean orangutans (*Pongo pygmaeus wurmbii*) of different age-sex classes utilize different strategies to cope with an unpredictable environment, as seen by differences in caloric intake in response to the availability of fruit (Harrison et al. 2010, Vogel et al. 2017). Additionally, the presence of adult conspecifics can dampen an individual's ability to forage. For instance, Harrison, et al. (2010) suggested the difference between party size (number of individuals within a specified distance) for flanged males compared to adult females in high fruit periods can lead to flanged males failing to meet their energetic requirements, while adult females meet their requirements more regularly. Studies like this, though, group adult females into a single category and fail to account for the variation in the nutritional costs throughout motherhood. Changes in movement (Lappan 2009, Ruivo et al. 2017), feeding (Goldberg et al. 1991, Murray et al. 2009), and the ability to take advantage of alloparenting (Raboin 2018) all impact a primate mother's nutritional costs and requirements across time. Alloparenting has yet to be observed in wild orangutans, and adult female orangutans are almost always found with a dependent (Mitani 1989, van Noordwijk et al. 2013b). The lactation period for orangutans is one of the longest known to animals, with infants nursing for up to eight years (Smith et al. 2017, van Noordwijk et al. 2018). Because females lactate for so long, orangutans do not time gestation or lactation with fruiting periods. Therefore, during lactation, the burden on a mother varies extensively as both the costs of maternal care and the availability of high-quality food items vary within the environment. It is important that researchers understand how

nutritional intake varies throughout motherhood and with fluctuations in the environment in a species with such a lengthy lactation period, as even smaller primate mothers with shorter lactation periods vary their nutritional and energetic intake (McCabe and Fedigan 2007, Dias and Rangel-Negrín 2015, Ruivo et al. 2017, Dias et al. 2018).

The Geometric Framework of Nutrition (GF) (Simpson et al. 1993) provides a simple, useful tool for investigating diet selection across varying ecological conditions by comparing the ratios of nutrients, such as the non-protein energy intake to available protein intake. This framework, also known as nutritional geometry, has helped answer questions regarding the relationships between nutrition, ecology, physiology, environment, and behavior in a wide variety of species (i.e. *birds*: Köhler et al., 2012, Coogan et al. 2018b; *fish*: Clements et al., 2009, Rowe et al., 2018; *insects*: Simpson et al., 2004, Lee et al., 2008; *mammals*: Coogan et al., 2018a, Nie et al., 2019; *humans*: Simpson and Raubenheimer, 2005) and provides new understandings for large-scale environmental problems associated with anthropogenic activities (Machovsky-Capuska et al. 2019). When plotted against each other, the selected macronutrients and the ratio between them form points in space, which can be averaged over either time or conditions to determine a linear representation of dietary intake known as a “rail”. Within primates, nutritional geometry has contributed greatly to understanding foraging decisions in the wild, including both the proximate and ultimate reasons for food selection (Raubenheimer et al. 2015, Lambert and Rothman 2015). In particular, two studies (Felton et al. 2009a, Rothman et al. 2011) demonstrate the value of nutritional geometry in showing specific strategies for regulating nutrient intake.. Felton et al. (2009) describe a protein-leveraging strategy found in spider monkeys (*Ateles chemek*), where available

protein intake is prioritized and relatively stable while other macronutrients (carbohydrates, lipids, fiber) vary extensively across seasons. Rothman et al. (2011), on the other hand, describes how mountain gorillas (*Gorilla beringei*) have a stable intake of non-protein energy, while protein varies with the amount of leaves consumed. Each study claims the routinely selected or prioritized macronutrient(s) is limiting, providing a simple spectrum based on food characteristics with protein optimizers on one end and non-protein energy optimizers on the other. Other primates, like the Diademed sifaka (*Propithecus diadema*), do not have a simple rule of compromise/ strict optimization of a macronutrient, and instead must vary their strategy depending on conditions like a gradient of habitat disturbance (Irwin et al. 2015). Maternal care could also potentially influence nutritional strategy, especially in species where the lactation periods and the complementary costs extend over multiple years.

Here, we investigate if there is variation in a mother's consumption of macronutrients across infant development and ask how a mother's caloric intake and macronutrient intake ratio (available protein to non-protein energy) vary with infant age across fruiting periods? We predict that:

- 1) When fruit availability is low, a mother will not be able to eat as many high-calorie fruits, regardless of her infant's age, resulting in reduced caloric intake compared to periods of high fruit availability. Additionally, available protein intake will increase while the intake of other remaining macronutrients will decline.
- 2) During periods of low fruit availability, a mother's caloric intake, carbohydrate intake, and macronutrient ratio (NPe:AP) will be lowest when she has a younger infant. As seen in Chapter 2, mothers with young infants are constricted in their behavior. While fruit is

scarce, female orangutans include a greater percentage of protein-dense foods (e.g., leaves) in their diets that are lower in overall calories (Chapter 2; Vogel et al., 2017). Thus, mothers are expected to be limited in their carbohydrate intake and utilize an energy conserving, time minimizing strategy.

3) During periods of high fruit availability, a mother's caloric intake, carbohydrate intake, and macronutrient ratio will be highest when she has a young infant. This is because mother orangutans greatly increase their ripe fruit consumption while they have young infants during higher fruiting periods (Chapter 2). Under these circumstances, mothers adopt an energy maximizing strategy and actively search for higher quality foods, like ripe fruits, until the maternal cost of an infant limits her foraging ability when her infant is around two years old. At this time, her macronutrient ratio will decrease, but still remain higher than during periods of low fruit availability.

3.2 Methods

3.2.1 Study Site

This project took place at Tuanan Orangutan Research Station (Tuanan; 2°09' S and 114°26' E) along the Kapuas Murung River in Central Kalimantan, Borneo, Indonesia. Tuanan is located in the Mawas Conservation Area, an area 3,090km² in size (van Schaik et al. 2005) and contains one of the world's largest remaining wild orangutan populations at approximately 3,500 individuals (Vogel, personal comm.). Researchers at Tuanan have continuously collected behavioral data on orangutans since July 2003. To date, there are over 125 genetically identified individuals at Tuanan, including nine habituated mother-infant pairs spanning every age range. Additionally, researchers at

Tuanan have collected monthly phenology data since 2003 on fruiting, flowering, and flushing patterns in 2.3ha of phenology plots (Vogel et al. 2015). These data are used to calculate the fruit availability index (FAI) in the habitat, a measure of the percentage of trees fruiting at a given time. While Tuanan does experience an annual high and low fruiting season, researchers still consider the fruiting cycle unpredictable because there is no known fruiting cycle for many plant species and the level at which fruiting fluctuates varies drastically from year-to-year (Harrison et al. 2016).

3.2.2 Behavioral Data Collection

We compiled full-day focal follows from 15 years of data ($n=1946$; 2003-2018) and 20,780 follow hours on nine Bornean orangutan mothers with dependent offspring (Table 3.1) following protocols from the Orang-utan Data Collection Standardization (<https://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html>; van Noordwijk, 2013). During each follow individual name, age class, focal activity, food item if applicable, height from ground, and associations with other individuals including distance between them were recorded in two-minute intervals. The average number of follows per month for this study was 11.67 ($\sigma = 7.53$), and no follow was included when it was the only follow in a month, unless it was part of a three day minimum follow period.

Table 3.1: Sample sizes across infant ages and fruit availability.

Infant Age	Fruit Availability			
	Total	High	Medium	Low
0-6months	269	30	113	126
6-12months	151	12	106	33
12-18months	146	24	69	53
18-24months	198	42	63	93
24-36months	310	86	135	89
36-48months	298	60	135	103
48-60months	214	24	108	82
60+months	360	58	161	141
Grand Total	1946	336	890	720

3.2.3 Macronutrient Analysis

Food item samples have been collected at Tuanan for nutritional analyses since 2004 and continue to be collected. Individual food items, after being judged for close similarity in size and maturation as to those eaten by orangutans, were collected from either the ground or tree from which an orangutan has been observed to feed (Knott 1998). At minimum three samples from each species at specific maturation stages were averaged to account for inter-tree variation (Houle et al. 2007, Rothman et al. 2012), since it is not possible or practical to sample from every individual tree of a given species at the field site. Samples were brought back to the station and processed as described in Vogel et al. (2015). A kerosene drying oven set to 40°C was used to dry the samples until they maintained a constant weight. Dried samples were then sealed, stored with silica gel, and sent to the Laboratorium Pengujian Nutrisi, LIPI-Bogor, Indonesia for nutritional analysis of crude protein, NDF, ash, and lipids under the supervision of Dr. Wartika R. Farida. To estimate crude protein, the laboratory used the Kjeldahl procedure to measure total nitrogen and then multiplied values by 6.25 (Pierce and Haenisch 1947). Since Indonesia

did not have the capacity to analyze available protein (AP) and export permits were not available, we estimated AP values from crude protein values using conversion coefficients used in previous studies on Indonesian food items (Conklin-Brittain et al. 1999, Vogel et al. 2017). The laboratory used the Soxtec method using Soxtec System HT2 to estimate crude lipid content (“Manual for Kjelttec 2300 Analyzer Unit” 2003). Neutral-detergent fiber content (NDF) was quantified through the detergent system of fiber analysis (Goering and van Soest 1970, Robertson and van Soest 1980). Total non-structural carbohydrates (TNC) were then calculated using the remaining difference (Conklin-Brittain et al. 2006). For invertebrate nutritional values, we used published values on tropical invertebrates (Oyarzun et al. 1996, O’Malley and Power 2014). All results are reported as 100% dry matter (DM; Conklin-Brittain et al., 2006).

3.2.4 Macronutrient Estimation

For each follow, we calculated intake for metabolizable energy (ME) of AP, TNC, lipids, and NDF content in food items using standard conversion factors in the following equation:

$$ME \text{ kcal}/100g \text{ DM} = (4 \times \%TNC) + (4 \times \%AP) + (9 \times \%lipids) + (0.543 \times \%NDF)$$

The conversion factor for NDF was derived experimentally with chimpanzees (Milton and Demment 1988), matches with known wild orangutan foods (Conklin-Brittain et al. 2006), and is the standard for more recent orangutan studies (Vogel et al. 2015, 2017). To calculate total caloric intake, macronutrient intake, and macronutrient ratio (NPe:AP) per day, we followed the procedures of Harrison et al. (2010), by first determining ME content of a whole food item using the field dry weight. We then multiplied the observed

feeding rate for the food item to find the ME intake per minute. Then, we multiplied the ME intake per minute by the length of the feeding bout, and summed the feeding bouts across a follow to calculate the daily intakes. To find NPe:AP, we summed the daily ME for TNC, lipids, and NDF and then divided it by the daily ME for AP (Simpson et al. 1993, Felton et al. 2009a). While over 85% of observed orangutan feeding bouts at Tuanan include food items analyzed for macronutrients, some food items lacked macronutrient estimates. For these items, we first tried to use values from a closely related species within the same genus that had similar physical characteristics. If this was not possible, we used the average value for that item type and stage of ripeness.

3.2.5 Statistical Analyses

For all analyses, we only included full-day nest-to-nest follows (i.e., the observer was with the orangutan from the time she left her morning nest to the time she entered her night nest), and we only included mothers with at least 50 follows. Additionally, before data analyses we controlled for outliers in the macronutrient estimations by calculating the mean and standard deviation for macronutrient intake estimates from all full-day follows at the field site, then excluding follows with any values above three standard deviations of the mean for total caloric intake ($\mu = 2763.1$, $\sigma = 1704.1$), available protein ME intake ($\mu = 292.7$, $\sigma = 176.7$), and non-protein ME intake ($\mu = 2470.4$, $\sigma = 1612.5$). We constructed generalized additive mixed models (GAMMs) using the *mgcv* and *gamm4* packages in R statistical software (Wood 2011, Wood and Scheipl 2017) to analyze the relationship between a mother orangutan's macronutrient intake, infant age (in years), and FAI. In every model, we included the interaction term between

the two independent variables. All predictor variables were fitted with spline smoothers, interactions with tensor product smoothers, and orangutan ID as a random effect (random intercepts) to prevent pseudo-replication across individual follow days (Harrison et al. 2009). When the interaction term was significant, we further explored the relationship in two ways: 1) by visualizing the interaction plots, and 2) by constructing GAMMs with a factor-by-variable design. Alongside the dependent variable and FAI was a term splitting infant age by three factors based from FAI quartiles. The three factors used were Low (smallest 25% of FAI values, $FAI < 2.30\%$), Middle (middle 50% of FAI values, $FAI = 2.30\% - 5.90\%$), and High (largest 25% of FAI values, $FAI > 5.90\%$). This design allowed us to see the relationship between the dependent variable and infant age during different periods of fruit availability. When reporting results, we refer to these models as factor-by-variable models.

3.3 Results

3.3.1 Food Items

Over the study period, mother orangutans consumed at least 675 identifiable food items, not including the water consumption or when a plant part could not be identified (Table 3.2, Figure 3.1). Fruit was the most common food item, with mothers consuming at least 356 species – ripeness – item combinations. Leaves were the second-most common food item, with mothers foraging on at least 186 species – ripeness – item combinations. Some of the rarer items mothers ate included bird eggs, honey, an unidentified small mammal, fungus, peat, and charcoal (noted as Other in Table 3.2). While fruits were the most common food category, the food items eaten the most were

young leaves from the legume *Leucomphalos callicarpus*, commonly known as akar kamunda. Akar kamunda young leaves were consumed in 21,279 feeding bouts, while akar kamunda half-ripe fruit (9,390 bouts) and flowers (5,752 bouts) were the second and third-most observed food items. Sixteen food items were observed eaten at least 1,000 times (Table 3.3) and 108 food items were observed between 100 – 1,000 times.

Table 3.2: *The number of identifiable food items found in a mother orangutan's diet, split up by the item's type.*

Item Type	# of Items
Bark	30
Flowers	59
Ripe fruit	121
Half-ripe fruit	124
Unripe fruit	111
Insects	13
Mature Leaves	51
Other	9
Pith	17
Other vegetation	55
Young leaves	85
<i>Total</i>	<i>675</i>

Table 3.3: Food items, listed by their common name, observed in at least 1,000 feeding bouts during the study period.

Common name	Item	High FAI	Medium FAI	Low FAI	Total Bouts
Akar kamunda	young leaf	3201	10856	7222	21279
Akar kamunda	half-ripe fruit	541	5471	3378	9390
Akar kamunda	flower	265	2381	3106	5752
Rayap	insect	885	1810	813	3508
Akar kecil	vegetation	273	1418	1633	3324
Akar kamunda	mature leaf	562	1464	1070	3096
Kamuning	young leaf	698	1331	1061	3090
Akar kamunda	unripe fruit	425	1008	1266	2699
Tutup kabali	half-ripe fruit	637	1499	75	2211
Mangis hutan daun kecil	half-ripe fruit	367	1318	373	2058
Tutup kabali	ripe fruit	1120	464	255	1839
Akar dangu	half-ripe fruit	187	1062	419	1668
Pantung	bark	85	465	1046	1596
Mangis hutan daun kecil	ripe fruit	539	711	56	1306
Pantung	pith	75	424	711	1210
Lewang	half-ripe fruit	167	824	106	1097
<i>Grand Total</i>		<i>20383</i>	<i>56806</i>	<i>36124</i>	<i>113313</i>

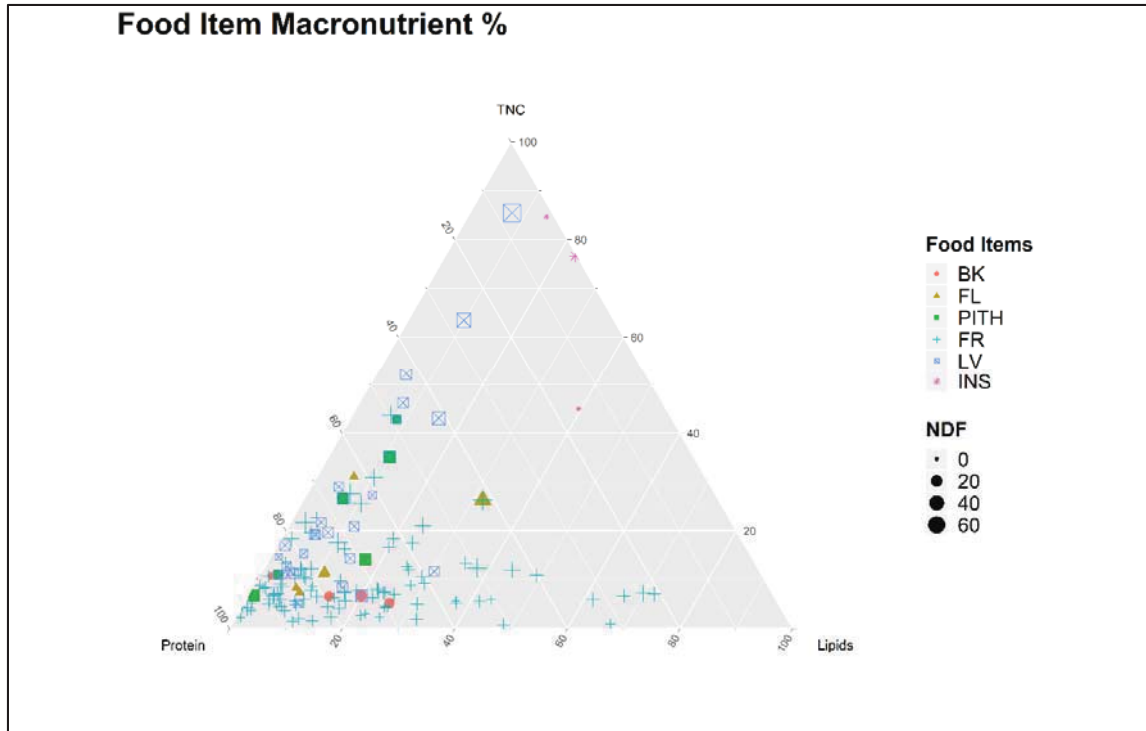


Figure 3.1: Estimated macronutrient percentages (derived from kilocalories) for each unique food item consumed by mothers during the study period. Available protein, total non-structural carbohydrates, and lipids are on the axes of the ternary plot, while neutral detergent fiber content is denoted by the size of the point. The type of the food item is denoted by the color.

3.3.2 Caloric Intake

On average, a mother orangutan consumed 2768.69 kilocalories/day ($\sigma = 1532.06$), however this varied significantly depending on the availability of fruit (Table 3.4, Table 3.5). We predicted that a mother would have lower caloric intake both in periods of low fruit availability (prediction 1) and when she has a young infant during these periods (prediction 2), while during high fruiting periods her caloric intake would be highest with a young infant (prediction 3). A mother's total estimated caloric intake

was significantly related to fruiting period, infant age during low fruit periods, and infant age during high fruit periods (Table 3.5, Figure 3.2). Overall, a mother's total estimated caloric intake and fruit availability were positively related between FAIs of 0-8, but then decreased after the maximum caloric intake at an FAI ~8. This is more than likely due to the small sample size at higher periods of fruit availability; still, the overall relationship is significantly positive and supports prediction 1. Infant age had a significant impact on a mother's total estimated caloric intake during both low and high fruiting periods but in opposite directions (Figure 3.2). By far the greatest change in a mother's caloric intake was during periods of low fruit availability. Here, a mother's intake decreased while she has an infant between birth and two years old, and reached a nadir of ~2,200 kcal/day with an infant around two years old. After this period, there was a sharp increase in her caloric intake that reached its maximum with an infant age of four years old, then stabilizing around the overall average of 2,768 kcal/day. Therefore, prediction 2 was supported, as a mother's caloric intake during low fruiting periods was significantly lower when she had a young infant. During high fruiting periods, a mother's intake increases steadily from birth to a maximum of over 3,000 kcal/day when she has an infant around three years old, supporting our prediction 3. Then, her intake decreases and stabilizes around the overall average when she has an infant that is five years old.

Table 3.4: Means for macronutrients across fruit availability.

Macronutrient (kcal)	Fruit Availability			
	Overall	High	Medium	Low
Total Calories	2768.689	2878.564	2941.351	2503.985
Avail. Protein	273.5605	257.3589	279.5347	273.7366
TNC	1699.093	1807.672	1801.024	1522.423
Lipids	510.7443	523.9783	565.682	436.6594
NDF	285.2916	289.5543	295.1097	271.1659

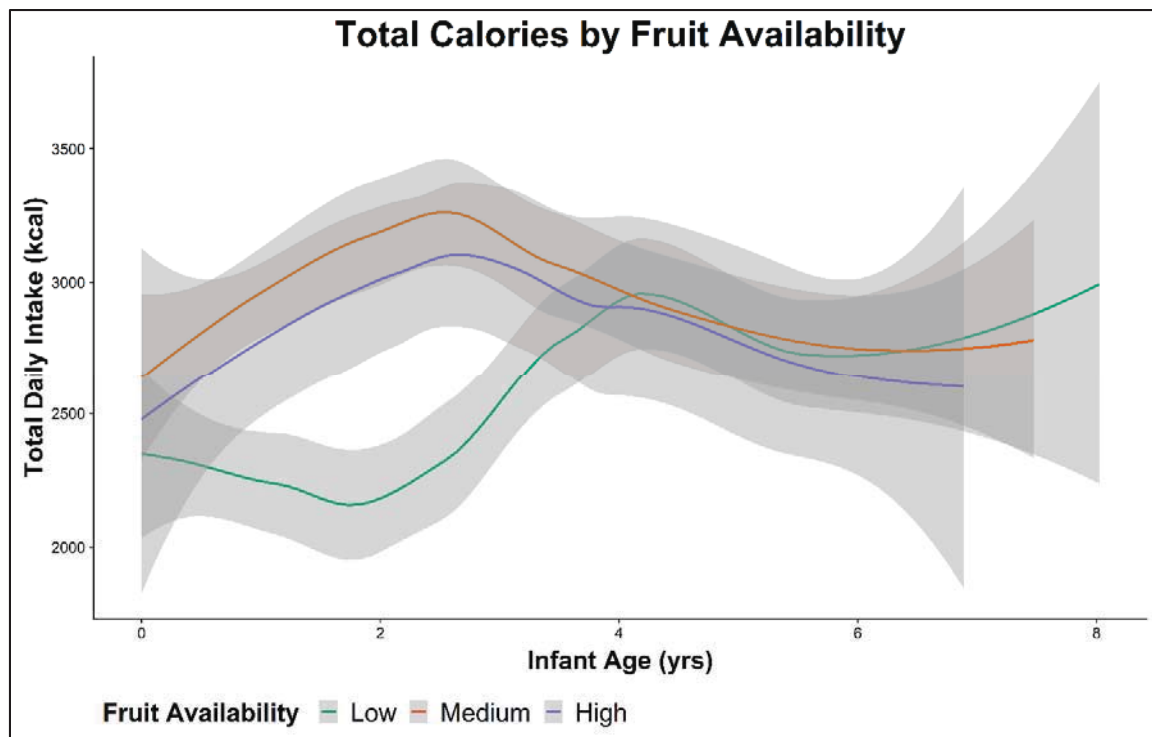


Figure 3.2: Graphical representation of the smoothing terms across both infant age and fruit availability for the total caloric intake GAMM factor-by-variable model. Note: this figure is representative of the model ran but does not include random slopes for individual orangutan ID.

Table 3.5: GAMM results for daily macronutrient intake, including total caloric intake

(N = 1946)

Model term	Total Calories			Avail. Protein			Carbohydrates		
	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
FAI	0.232	1.429	1.000	<0.0001	20.78	1.000	0.405	0.694	1.000
Inf. Age	0.144	2.149	5.530	0.011	2.747	4.639	0.005	3.405	6.336
FAI * Inf. Age	<0.0001	8.690	10.400	<0.0001	4.715	11.749	<0.0001	6.639	10.17
r ²	0.066			0.051			0.0634		
AIC	33886.21			24867.26			32495.53		
FAI	<0.0001	20.80	4.703	<0.0001	8.964	3.569	<0.0001	20.32	3.870
Inf. Age-High FAI	0.045	3.178	2.084	0.731	0.118	1.000	0.3374	0.921	1.000
Inf. Age-Mid FAI	0.263	0.814	1.592	0.0003	5.168	4.503	0.052	3.796	1.000
Inf. Age-Low FAI	0.0003	4.779	4.462	0.0003	6.252	3.523	<0.0001	6.625	5.022
r ²	0.058			0.0386			0.0521		
AIC	33898.50			24879.67			32507.37		
Model term	Lipids			NDF			NPe:AP		
	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
FAI	<0.0001	10.49	5.514	0.00015	5.056	5.192	0.0007	11.50	1.000
Inf. Age	0.052	3.767	1.000	0.005	7.757	1.000	0.005	7.743	1.000
FAI * Inf. Age	0.069	1.910	4.717	<0.0001	5.786	7.142	<0.0001	7.088	15.89
r ²	0.0446			0.042			0.094		
AIC	29772.27			25630.72			12487.32		
FAI	<0.0001	12.17	5.207	<0.0001	8.271	5.230	<0.0001	27.99	3.443
Inf. Age-High FAI	0.0003	5.099	3.912	0.0002	7.196	3.042	0.518	0.418	1.000
Inf. Age-Mid FAI	0.086	1.955	3.295	0.014	2.775	4.446	<0.0001	6.742	5.678
Inf. Age-Low FAI	0.164	1.819	3.190	0.015	3.511	2.564	0.002	3.961	4.328
r ²	0.0469			0.039			0.076		
AIC	29763.27			25645.51			12522.24		

3.3.3 Macronutrient Intake

Overall, a mother orangutan consumed an average of 273.56 kcal/day from available protein ($\sigma = 147.01$), 1699.09 kcal/day from total nonstructural carbohydrates

($\sigma = 1064.82$), 510.74 kcal/day from lipids ($\sigma = 522.73$), and 285.29 kcal/day from neutral detergent fiber ($\sigma = 179.09$). We predicted that a mother's available protein intake would be negatively correlated with fruit availability, while her carbohydrate, lipid, and fiber intake would be positively related with fruit availability (prediction 1). We also predicted that during periods of low fruit availability, a mother's carbohydrate intake would be lowest when she had a young infant (prediction 2), but during high fruit periods her carbohydrate intake would be highest with a young infant (prediction 3). Overall, a mother's protein intake declined as fruit availability increased, supporting prediction 1. Conversely, her carbohydrate, lipid, and fiber intake increased significantly between FAIs 0-8, also supporting prediction 1 (Table 3.5). In predictions 2 and 3, we expected to see a mother's carbohydrate intake vary differently with the age of her infant, depending on fruit availability. In support of prediction 2, her carbohydrate intake was at its lowest during periods of low fruit availability while she had an infant around two years old (Table 3.5, Figure 3.3). Additionally, during low fruit periods, mother increased her available protein intake when her infant was older. We did not find support for prediction 3. Overall, a mother's carbohydrate intake generally increased as her infant aged, but this was primarily driven by the reduction in intake with a young infant during low fruit periods. When fruiting was high, a mother did not vary her intake depending on the age of her infant (Table 3.5). However, during high fruit periods, a mother's fiber consumption was highest while she had a younger infant (Table 3.5, Figure 3.3).

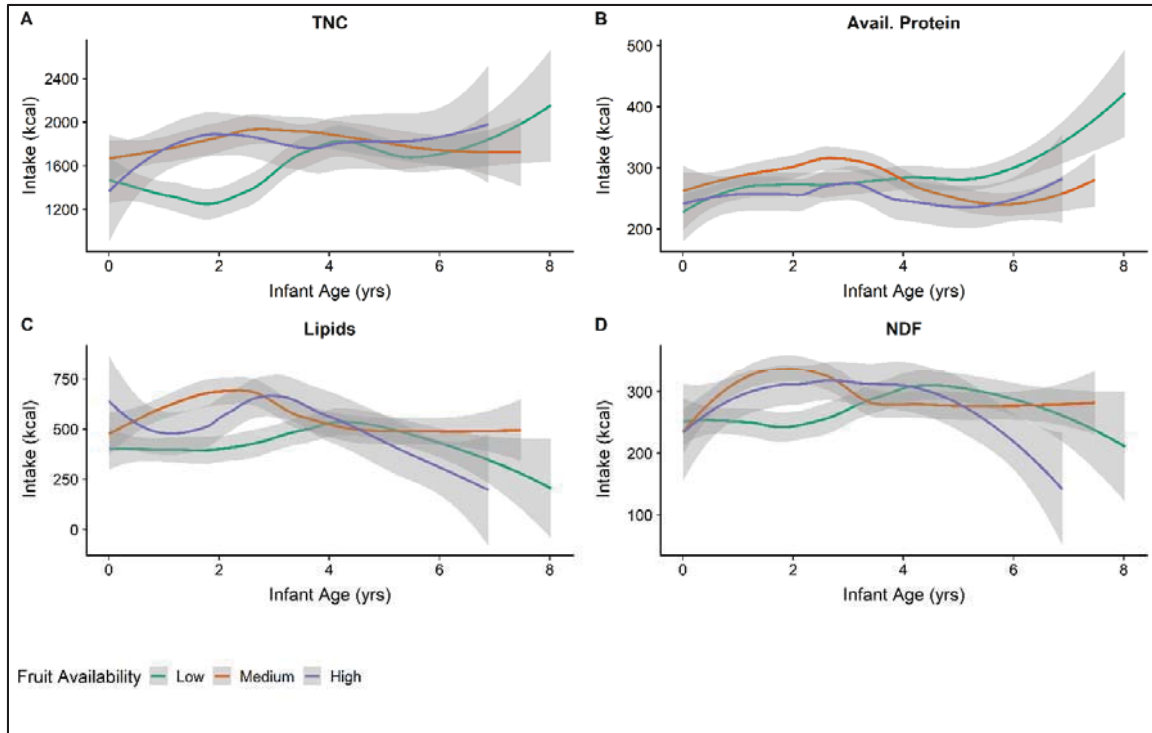


Figure 3.3: Graphical representations of the smoothing terms for the GAMM factor-by-variable models across both infant age and fruit availability for daily a) total nonstructural carbohydrates, b) available protein, c) lipids, and d) neutral detergent fiber. Note: these figures are representative of the models ran but do not include random slopes for individual orangutan ID.

3.3.4 Macronutrient ratio variation

The mean ratio of NPe:AP for a mother across the study period was 10.33 ($\sigma = 6.21$). We predicted that during low fruiting periods, a mother's macronutrient ratio would be lowest when she had a young infant (prediction 2), but during high fruiting periods her macronutrient ratio would be highest with a young infant (prediction 3). Overall, a mother's macronutrient ratio increased significantly with fruit availability, but decreased significantly with the age of her infant (Table 3.5). However, when run in the

factor-by-variable model design, a mother's macronutrient ratio and the age of her infant were only significantly related in low and medium fruit periods (Table 3.5; Figure 3.4). During the low fruit periods, a mother with an infant near two years old had the smallest NPe:AP, supporting prediction 2. This decrease started immediately after birth. After this nadir, a mother's ratio then increased and eventually peaks when she had an infant around four years old at a ratio similar to that of the overall average of mothers with four-year-old infants during other fruiting periods. Conversely, during medium fruit periods, a mother had a relatively stable intake ratio of macronutrients until her infant was around three and a half years old, then there was an overall steep increase and a plateau in a mother's macronutrient ratio with infants between five and six years old. Prediction 3 was not supported, as there is no relationship between a mother's macronutrient ratio and the age of her infant during periods of high fruit availability (Table 3.5).

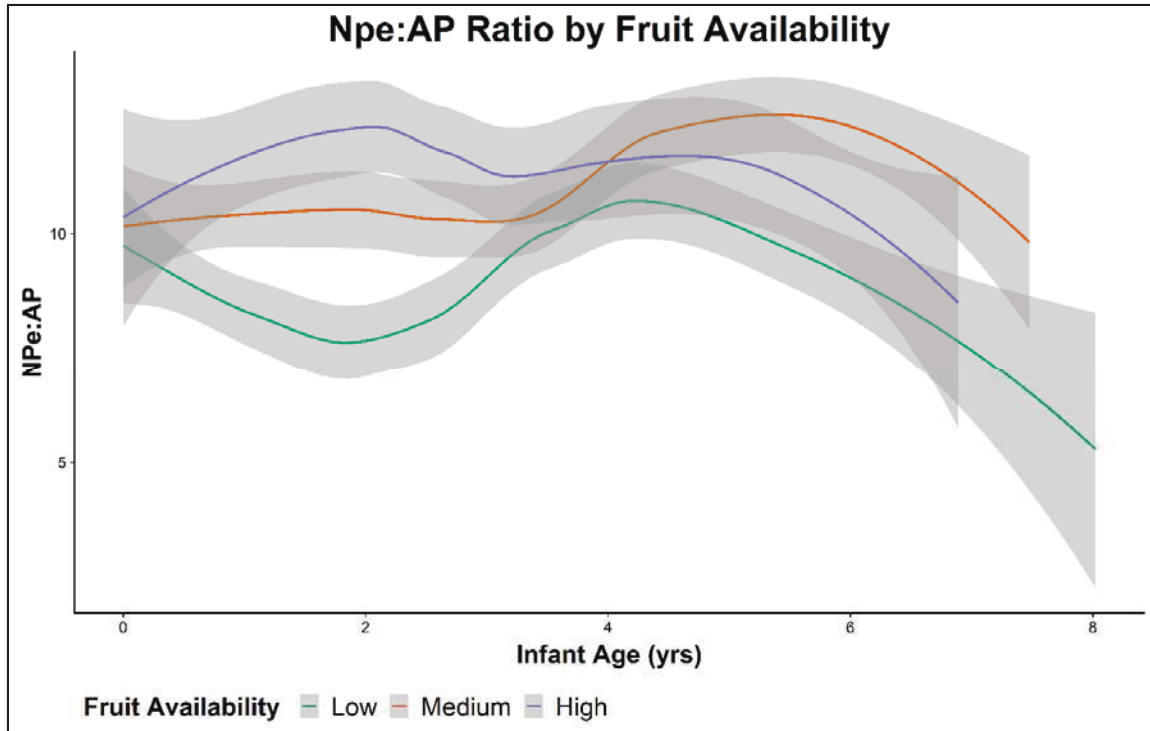


Figure 3.4: Graphical representation of the smoothing terms across both infant age and fruit availability for the NPe:AP GAMM factor-by-variable model. Note: this figure is representative of the model ran but does not include random slopes for individual orangutan ID.

Given that variation in macronutrient balance exists among mother orangutans across two of the three infant age – fruit availability combinations (not during high fruiting periods), we predicted NPe:AP intake from our constructed factor-by-variable models using the “predict” function in the Stats R package (R Core Team 2019) for mothers across multiple infant age – fruit availability combinations to aid our discussion (Table 3.6, Figure 3.5). From the predicted values, during high fruiting periods, a mother’s NPe:AP intake is remarkably stable across infant ages. Mothers with infants 4 years old have fairly similar predicted ratios throughout fruit availability, except during

the lowest periods. A mother in higher fruiting periods has a macronutrient ratio around 11.5, but the ratio decreases during the lowest fruit availability periods. What particularly stands out is the predicted difference between mothers with a two-year-old infant during high and low fruiting periods (Figure 3.6). Here, during a period with an FAI of 10, a mother is predicted to have a NPe:AP almost twice as large as a mother during an FAI period of 0.5 (FAI 10 = 11.87, FAI 0.5 = 6.40, $\Delta = 5.47$).

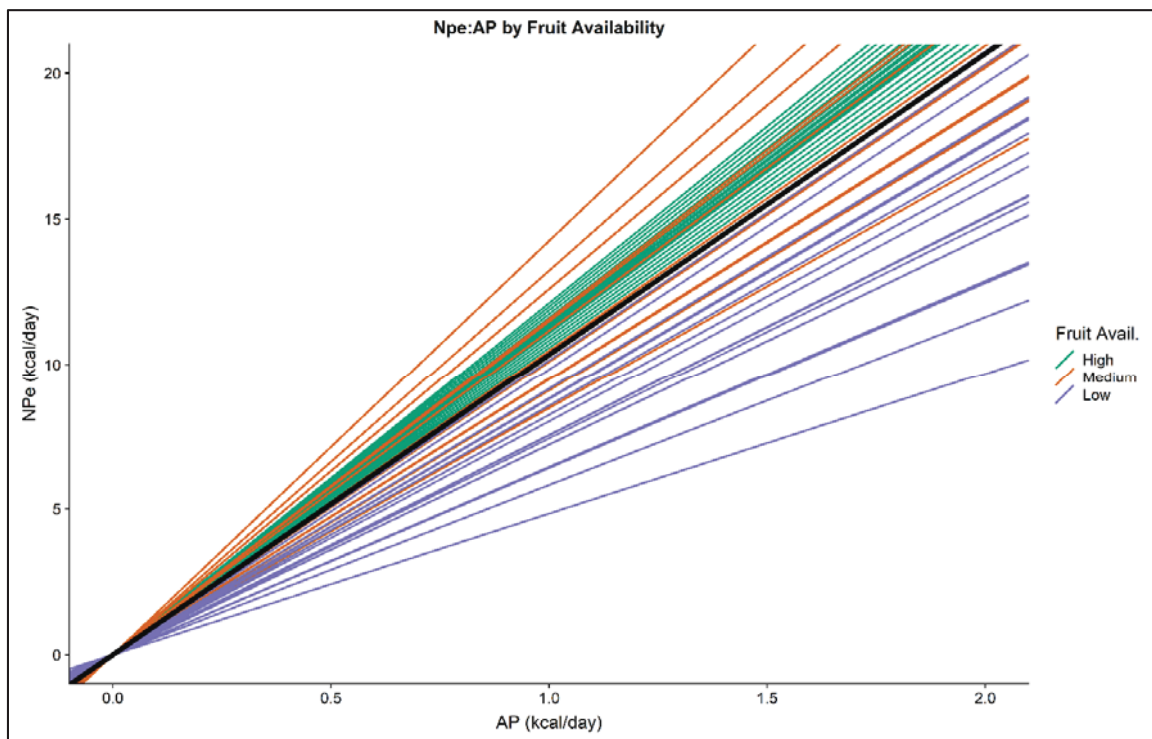


Figure 3.5: Predicted NPe:AP rails for infant age – fruit availability combinations, based on the GAMM factor-by-variable model. The black rail represents the overall mean for the sample.

Table 3.6: Predicted NPe:AP for infant age – FAI combinations, based on the GAMM factor-by-variable model.

		FAI Input Values					
		High		Medium		Low	
		10	7	5	3	2	0.5
Infant Age Input (yrs)	0.01	12.118220	11.572030	10.150947	9.129899	9.827989	8.227377
	1	11.995400	11.449210	10.473945	9.452897	8.802975	7.202362
	2	11.871340	11.325150	10.093750	9.072702	8.004236	6.403623
	3	11.747280	11.201080	10.118769	9.097721	9.135971	7.535359
	4	11.623220	11.077020	11.492220	10.471172	10.372011	8.771398
	5	11.499160	10.952960	14.253124	13.232076	10.147053	8.546440
	6	11.375090	10.828900	12.600008	11.578960	9.121972	7.521260
	7	11.251030	10.704840	11.166655	10.145607	7.416966	5.816353

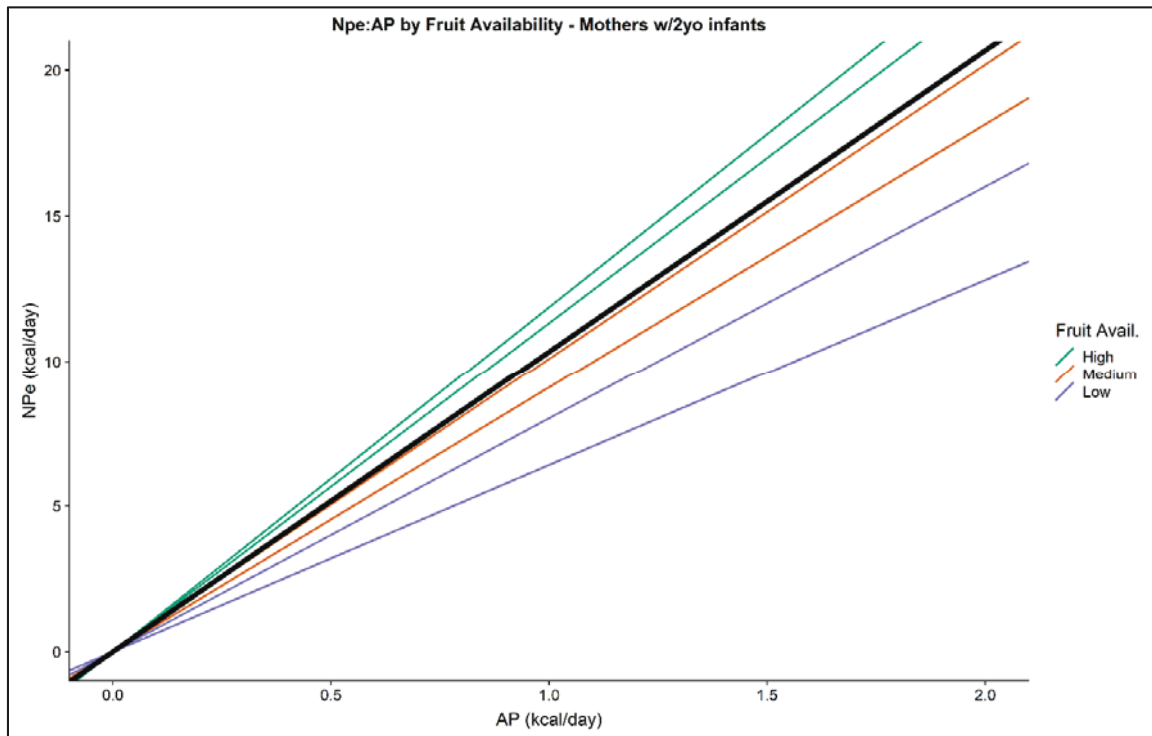


Figure 3.6: Predicted NPe:AP rails for mothers with two-year-old infants at various FAI values, based on the GAMM factor-by-variable model. Only mothers in the high fruiting period have rails that are greater than the sample mean rail.

3.4 Discussion and Conclusions

3.4.1 Caloric Intake and Macronutrient Intake Variation

Overall, a mother's total caloric intake was lowest during periods of low fruit availability regardless of her infant's age, supporting prediction 1 and agreeing with previous research investigating nutritional intake differences among orangutan age-sex classes (Vogel et al. 2017). In other studies of primate maternal nutrition, there is either remarkably little effect of seasonality or no discussion of seasonal influences on nutrition throughout lactation (McCabe and Fedigan 2007, Lappan 2009, Webb 2017, Dunham and Rodriguez-Saona 2018). Orangutan maternal nutrition and the strategies used could be unique. They don't fit into traditional capital, income, or seasonal breeding models because lactation period lasts across multiple years in a relatively marginal quality tropical forest for species that prefer fruit (van Schaik and Pfannes 2005, van Noordwijk et al. 2013b). A solitary mother that lactates across multiple seasons must supplement nutritional intake (income breeding) with stored energy reserves (capital breeding) that she builds when food availability and her activity levels allow her to do so. Additionally, mother orangutans do not have significant help of conspecifics, as found in primate species with similar multiyear lactation periods, like humans (*Homo sapiens*; Van Noordwijk et al. 2013) or chimpanzees (*Pan troglodytes*; Emery Thompson et al. 2012a, Bădescu et al. 2016). Previous work hypothesized that multiyear lactation with long overlaps in nursing and solid food consumption, similar to that observed in wild orangutans, is an ancestral condition of hominins before the divergence of *Homo sapiens* (van Noordwijk et al. 2013a). In order to maintain fitness levels through energetically challenging periods, though, modern humans have evolved a strategy that relies on other

individuals to reduce the costs imposed on the mother (infant handling, vigilance, high-calorie provisioning, etc.; Kaplan et al. 2000, Alvarez 2000, Hrdy 2009). Because of the high level of conspecific assistance, both modern human lactation periods and interbirth intervals are much shorter than expected for their body and brain size (Walker et al 2006; Robson and Wood 2008; van Schaik and Isler 2012). Wild chimpanzees are similar, as they also exhibit multiyear lactation (weaning age is around four years old; van Schaik and Isler 2012), yet alloparental handling reduces a mother's lactation effort and consequently the energetic costs of lactation (Bădescu et al. 2016). While many large-bodied primates must rely on multiple seasons to support offspring and development, much of the effort is post-lactation (Emery Thompson 2013a, van Noordwijk et al. 2013a), orangutan mothers are the only species that face environmental energetic challenges while being the sole provider for their infants.

During low fruit periods, a mother's caloric intake and carbohydrate (TNC) intake was lowest when she had a younger infant, supporting prediction 2 that a mother will have lower intake of foods with more accessible energy while she has a young infant. Prediction 3, which predicted that in periods with high fruit availability a mother's caloric intake, carbohydrate intake, and macronutrient ratio will be highest when she has a young infant, was only partially supported. During high fruit periods, a mother's caloric intake varied as her infant aged, but her macronutrient intake remained stable and did not change. The opposing directionality of a mother's change in caloric intake with younger infants is interesting because other primate species are the most energetically constrained when mothers have younger infants but they utilize differing strategies to buffer from this challenging period (*Symphalangus syndactylus*: Lappan, 2009; *Alouatta pigra*: Dias et

al., 2011, 2018; *Pan troglodytes*: Thompson et al., 2012; *Colobus angolensis*: Dunham and Rodriguez-Saona, 2018). Our previous research suggests maternal cost, which includes both the time and energy needed for a mother to invest in a specific offspring (Trivers 1972) and behaviors that overall improve an offspring's chances of survival (Clutton-Brock 1991), is greatest when an infant is around two years old (Chapter 2). A mother orangutan seems to be utilizing multiple strategies to buffer the effects of variation in fruit availability during this period by either 1) reducing caloric intake and minimizing activity (energy expenditure), or 2) maximizing energetic intake by being a more active forager (Chapter 2). During periods of medium fruit availability, a mother with a young infant may utilize either strategy and this may explain the lack of significance in the model. After the period of greatest maternal cost, a mother's caloric intake is remarkably similar, regardless of fruit availability, further supporting the idea that mothers with young infants are much more constraint.

Vogel et al. (2017) found that, overall, adult female TNC increased as fruit availability increased. Our analyses show otherwise and show there is no change in TNC intake across fruiting unless you take infant age into account. One potential explanation is while we included infant age in the model, Vogel et al. (2017) did not. Additionally, Vogel et al. (2017) structured their model around all age-sex classes, so data on other individuals with varying foraging behavior, such as flanged males, influenced the result. We see that a mother's non-structural carbohydrate intake remains relatively high throughout both medium and high fruiting periods, which when paired with our caloric intake results presented here and previous results on maternal behavior (Chapter 2) suggest a mother is able to maintain energetic homeostasis while spending the required

energy to seek out high-quality food items. This is not the case during low fruit periods, when we see a mother's TNC intake is lower when she has a young infant. Here, a mother slowly increases her protein intake while facing this carbohydrate deficit, with the largest increase while she has an older infant. Protein intake also increases during medium fruit periods, but this is only while her infant is around two to three years old. Protein is an essential component for milk, as it provides the amino acids needed for an infant's growth and immune system function (Hinde and Milligan 2011), so periods of increased protein intake for a mother might relate to critical growth periods of infant development. However, previous work on humans and cattle shows that changes in dietary protein intake do no result in significant changes in milk protein concentration (Emery 1978, Nommsen et al. 1991, Ballard and Morrow 2013). A mother might also be using the protein for her own maintenance and immune activity, which is presumably the most important during very challenging conditions, like an extended dearth in preferred food availability. Alternatively, both of these increases could be the result of a behavioral change due to infant age, albeit for different reasons. During medium fruiting periods, a mother's increase in protein intake occurs during her infant's most taxing age, restricting her diet. During periods of low fruit availability, however, this increase is mainly while a mother has an older infant, and is potentially due to conflicts in foraging decisions between the two individuals. An older infant is much more capable of making individual foraging decisions (Schuppli et al. 2016), and is potentially at odds with a mother's foraging goals while leading up to weaning (Trivers 1972).

Additionally, it is possible that a mother is acquiring more energy from NDF than previously thought via her gut microbiome, which breaks down dietary fiber and

produces short chain fatty acids (SCFA; Flint and Bayer, 2008). Research investigating the importance of this process in wild primates is still in its infancy (Amato 2013), but previous controlled studies show that SCFA produced by the gut microbiome can be used as an energy source in the body (Mackie 2002, Amato 2016). During high and medium fruiting periods, a mother increases her NDF intake when her infant is around two years old, the most taxing age, so it is possible that fiber intake does contribute to a mother's energy balance during lactation. Going forward, maternal care, including the costs of lactation, is an important variable that must be considered when investigating the diet and gut microbiome of a mammal species. This is especially true for mammals with extended periods of lactation, like orangutans, and future research on similar study systems should use a finer scale of investigation that includes both infant age and preferred food availability.

3.4.2 Macronutrient Ratio as a Tool for Understanding Variation

While a mother seemingly starts with a macronutrient ratio near the overall sample average of 10.33 when her infant is born, this quickly changes depending on fruit availability. In support of prediction 2, a mother's macronutrient ratio was lowest when she had a younger infant. Specifically, a mother's NPe:AP was lowest when she had an infant around two years old during low fruit availability periods. Behaviorally, in these conditions a mother will rest more and eat lower quality yet more abundant foods like bark, pith, flowers, and mature leaves (Chapter 2). With this dietary switching behavior, one would expect a lower macronutrient ratio as NPe intake is reduced and protein intake is increased. During medium periods of fruit availability, a mother has a stable but lower

than average NPe:AP while with a young infant, which then increases when her infant is around three years old. Our previous activity budget and dietary profile research indicate that during medium fruit availability periods, a mother with an infant older than three increases her time spent moving, daily path length, and time spent eating fruit while also decreasing the amount of time spent feeding on leaves. These behaviors agree with previous studies that showed mother orangutans are less behaviorally constrained by their infants around this age (van Noordwijk et al. 2009, Chappell et al. 2015), and fits with the observed increase in a mother's NPe:AP during medium fruiting periods. While there was significant variation during low and medium fruiting periods, a mother's macronutrient ratio remained stable during high fruiting periods, not supporting prediction 3. Our predicted macronutrient ratios help us understand this more.

Within the predicted values, there is also little variation in a mother's ratio during the high fruiting period when compared to medium and low periods of fruit availability. This could suggest that the optimal macronutrient ratio for mother orangutans falls within this area, an NPe:AP of around 11.5, and is similar to the observed foraging behavior in locusts, where when high quality food is available, individuals only feed until their nutritional targets are met and do not over-satiate (Simpson and Raubenheimer 2000). Other primate mothers, such as the Angola colobus (*Colobus angolensis*), have a confined macronutrient ratio between both seasons and lactation stage, suggesting they are not inhibited by either environmental variation or maternal care (Dunham and Rodriguez-Saona 2018). A mother orangutan with an older infant in high periods of fruit availability has the least maternal care associated with her, as she has a capable offspring and a relatively large selection of preferred foods to choose from. Still, she has

significantly lower caloric intake compared to a mother with a younger infant and a constricted macronutrient balance, suggesting that a mother has higher energy demands when their infants are younger. Orangutans are the only primate besides humans known to build fat stores during periods of high fruit availability (Knott 1998). Therefore, a second and perhaps more likely explanation for the lack of variation in a mother's macronutrient ratio during high fruit periods is this ratio may be the best for building fat stores to buffer from future periods of low food availability and/or when she gives birth to a new infant. Our model results demonstrate that a mother has a reduced caloric intake when she is most taxed by young infants during low fruit periods, and building fat stores is a potential adaptation to safeguard from these challenging periods. Indeed, we see much more variation in a mother's predicted macronutrient ratios as fruit availability decreases, including points where a mother's NPe:AP during medium fruiting periods is greater than those during high periods (Figure 3.5). The lower NPe:AP and the large difference in ratios between the highest and lowest FAI values occur at the same point as the time of maximal maternal care observed through mother orangutans' activity budgets and general dietary profiles (Chapter 2). Activity budgets and general dietary profile research is useful, but does not provide enough evidence to determine if a mother is either seeking out protein while caring for a young infant or if macronutrient intake is limited by the available food in the habitat. Collectively with research on activity budget, these results suggest that a mother orangutan with a two-year-old infants does not vary her macronutrient intake when there is enough preferred food available, and only when the availability of these food items is reduced does her NPe:AP fluctuate. If a mother was specifically selecting high-protein foods while she has a young infant, one would expect

protein content in milk to vary over the lactation period and dietary protein to contribute significantly to the energy available in milk. However, larger primates produce milk relatively less dense in protein than smaller mammals (Power et al. 2002, Hinde and Milligan 2011), relative protein density in milk does not change in humans across the first year of lactation (Mitoulas et al. 2002), and protein is not correlated with milk energy density in primates (Hinde and Milligan 2011). Additionally, Bornean orangutans have one of the lowest percent energy from protein (kcal/g) in milk (Hinde and Milligan 2011), so it is highly unlikely that a mother is seeking out protein while with a young infant. Instead, a mother is limited by what is available to her and potentially builds fat reserves when she can to support the cost of lactation and maternal care. Measuring a mother's fat catabolism throughout the conditions explored here, as done in Chapter 4, would provide another line of evidence to determine if mothers are actually building fat reserves in high quality periods and utilizing them during the low periods we see in this analysis.

3.4.3 Conclusions

Multiple primate species alter their caloric and macronutrient intakes in response to fluctuations in preferred food availability, whether due to environmental seasonality or habitat disturbance (Conklin-Brittain et al. 2006, Irwin et al. 2014, 2015, Koch et al. 2017). This study demonstrates that there is a strong interaction between intakes, preferred food availability, and the age of an orangutan mother's infant, something that most studies do not take into consideration when investigating maternal nutrition. Orangutan mothers provide a unique study system to investigate this interaction as they

have a large dietary repertoire (675 unique food items observed over 15 years of data collection) and an extended lactation period that spans multiple unpredictable fruiting cycles (van Noordwijk et al. 2013b). From this project, there are several key insights into orangutan maternal nutrition and foraging. First, a mother's total caloric intake increases during high fruiting periods but decreases during low fruiting periods when she has a young infant. Second, a mother's carbohydrate intake is significantly lower during low fruiting periods when a mother has an infant around two years old, but doesn't vary when fruit availability is high or medium. Finally, a mother's NPe:AP is relatively consistent across infant ages during high fruiting periods, but significantly less and much more variable during low fruiting periods. Together, these results suggest that orangutan mothers utilize different strategies to survive with infants depending on the availability of fruit in the environment, given constraints in food item selection. In periods of low fruit availability, a mother cannot sustain a high caloric or carbohydrate intake, and instead forages on a number of less-preferred food items while also reducing her activity (Chapter 2). During periods of high fruit availability, a mother maintains a high but controlled intake of calories and non-protein macronutrients, even when she has a young infant. This potentially allows her to build up her fat stores for more depauperate periods. Future research on maternal foraging behavior needs to consider the interaction between infant age and preferred food availability, otherwise important patterns may be masked.

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Chapter 4. Combining multiple lines of noninvasive physiological evidence from urinary metabolites to infer energetic condition in wild mother orangutans (*Pongo pygmaeus wurmbii*)

4.1. Introduction

The endocrine system is vital for allocating energy and mediating the utilization of metabolic resources needed for reproduction, including lactation (Ellison 2003). Physiological indicators of energetic condition should therefore help inform researchers about a mother's energetic strategy during reproduction by providing information on her energy balance (the difference between caloric intake and expenditure) and energy status (the amount of stored energy; Emery Thompson, 2017). These are especially vital in field studies, where it is not always possible to collect pertinent data relating to the energetics of a population or species. Field researchers rely on noninvasive techniques in an attempt to minimize ethical issues faced in monitoring species that are, among others, low in population density, protected by restricting regulations such as the amount of time a researcher can observe an individual or capturing them (van Noordwijk et al. 2012), or those species that exist in habitats that present observational challenges to the researcher (Fedigan 2010). Additionally, the quantity of samples collected might not be enough to run multiple physiological analyses on the same sample, or there might be sample export restrictions from habitat countries that limit the amount of sample available in the lab, presenting added layers of complexity to the data analysis. One possibility for researchers facing situations where it is difficult to collect data is combining multiple lines of

biomarker evidence, analyzed both *in situ* and in the laboratory, with behavioral observations to elucidate as much information as possible about their study population.

Producing accurate estimates of energetic balance can be particularly difficult for field ecologists, as the two primary options are tracking an individual's weight or estimating energy intake and expenditure. Tranquilizing individuals to take weight estimates is invasive (Fedigan 2010), and calculating estimated intake/expenditure is tedious at best, given the amount of detailed observation needed over an extended period of time, alongside multiple forms of supplemental data that each require their own analyses (Altmann and Samuels, 1992; Rothman et al., 2011; Irwin et al., 2014; Vogel et al., 2017; Chapter 3). Glucocorticoids, and specifically cortisol in primates, are part of the stress response system and produced through the hypothalamic-pituitary-adrenal axis. One primary function of cortisol is regulating glucose availability and it has been measured in individuals experiencing energetic stress (Saplosky 1992, Gesquiere et al. 2008). Previous research has also demonstrated that urinary cortisol levels are related to foraging effort (van Schaik et al. 1991). While cortisol levels also vary with many other factors, such as sociality and group size (Muller and Wrangham 2004, Pride 2005), long-term monitoring of it should capture at minimum the influence of energetic status on the stress response (Emery Thompson 2017). Insulin is vital in regulating glucose uptake in the body and aids in building fat and glycogen energy stores (Foster and McGarry 1992). However, previous research only measures insulin concentration in serum, making it extremely invasive to monitor in populations (Kemnitz et al. 2002). Urinary C-peptide of insulin (UCP) is a connecting peptide that is cleaved from proinsulin to create insulin in the body, and is produced in equimolar amounts to insulin (Sherry and Ellison 2007,

Emery Thompson and Knott 2008). This, along with the fact that it is cleared from the body in urine at the same rate as its production, instead of operating on a circadian rhythm like cortisol, make it an ideal biomarker to track an individual's energy balance.

Estimating energy status in wild primates also presents difficulties, as it has traditionally been estimated by invasively measuring physical factors such as skin folds or body mass index (Emery Thompson 2017). Instead of measuring energy status directly, researchers can noninvasively monitor biomarkers that signal the utilization of energy stores. The measurement of ketone bodies (ketones) is one method of noninvasively tracking energy status in mammals, and have been successfully measured in orangutans (Knott 1998). Ketones are produced when an individual experiences severe carbohydrate shortages and the body catabolizes its fat reserves (Emery Thompson 2017). Ketones are also one of the few biomarkers that are easily categorically measured *in situ*. Gluconeogenesis is the production of glucose from non-carbohydrate sources (Veldhorst et al. 2009). The concentration of urea in an individual's urine is an indicator of nitrogen catabolism from gluconeogenesis and/or dietary protein, and has been used to analyze multiple species' body condition in specific environmental conditions (Barboza and Parker 2006, Vogel et al. 2012b, Gustine et al. 2012). Previous research on orangutans states that, in general, urea production increases with absolute dietary protein intake, which was highest during periods of high fruit availability in one study (Vogel et al. 2012a), but also lower during periods of high fruit availability in another (Vogel et al., in prep). Therefore, urea can be a useful biomarker to determine if a mother's energy balance and status from protein sources are affected during her infant's development.

Orangutan mothers have one of the longest lactation periods of any mammal on the planet, with infants nursing for up to eight years (Smith et al. 2017). Across motherhood in orangutans, individuals experience vast fluctuations in the availability of fruit, their preferred food, while providing milk for a slow-growing infant (van Noordwijk et al. 2013b). Because of their extended lactational period, it is difficult to assess how the energetic condition of mother orangutans varies, including how it varies across the interaction between the age of an infant and the availability of food in the environment. Previous research shows that orangutans, regardless of age-sex class, catabolize fat reserves (Knott 1998), recycle protein (Vogel et al. 2012b), and exhibit variation in energy balance (Emery Thompson and Knott 2008), but there is little research on how these processes vary throughout motherhood.

The goal of this study is to bring together multiple forms of noninvasive physiological evidence to understand what the critical energetic periods are for lactating wild mother orangutans. Specifically, we investigate if a mother's energetic status, as measured through physiological indicators, varies significantly with the availability of fruit in the environment, the age of her infant, and her ingested calories. We predict that:

1. When fruit is scarce and caloric intake is reduced, a mother will have lower concentrations of UCP, indicating a lower energy balance. A mother will have higher levels of cortisol, reflecting increased nutritional stress, and urea, because she relies more on protein as an energy source in low fruiting periods. Additionally, we expect a mother will have a greater likelihood of ketone detection in their urine.
2. During high fruiting periods, a mother will have elevated levels of UCP, reflecting her increased food intake and consequential increase in energy balance. Her urea and cortisol

levels will be reduced because she experiences less nutritional stress and lower levels of gluconeogenesis as most of her energy is derived from carbohydrates. Additionally, she will have a lower likelihood of excreting urinary ketones because she is relying less (or not at all) on fat reserves.

3. When a mother has a young infant, she is more likely to be in a negative energy balance state because in addition to consuming sufficient calories to meet both her and her infant's caloric demands, she is behaviorally limited in her foraging ability.

Therefore, her UCP levels will be reduced, and because she will potentially rely on her body fat stores more, her probability of excreting ketones will be increased. Additionally, both her cortisol and urea levels will be elevated because she is forced to forage on more proteinaceous foods containing fewer relative calories.

4.2 Methods

4.2.1 Study Site

This project took place between March 2009 – April 2018 at Tuanan Orangutan Research Station (Tuanan; 2°09' S and 114°26' E) along the Kapuas Murung River in Central Kalimantan, Borneo, Indonesia. Tuanan is located in the Mawas Conservation Area, an area 3,090km² in size (van Schaik et al. 2005) and contains one of the world's largest remaining wild orangutan populations at approximately 3,500 individuals (Vogel, personal comm.). Researchers at Tuanan have continuously collected behavioral data on orangutans since July 2003. To date, there are over 125 genetically identified individuals at Tuanan, including nine habituated mother-infant pairs spanning every age range. Additionally, researchers at Tuanan have collected monthly phenology data since 2003

on fruiting, flowering, and flushing patterns of 1,868 trees in 2.3ha of phenology plots (Vogel et al. 2015). These data are used to calculate the fruit availability index (FAI) in the habitat, a measure of the percentage of trees fruiting at a given time. While Tuanan does experience an annual high and low fruiting season, researchers still consider the fruiting cycle unpredictable because there is no known inter-annual fruiting cycle for many plant species and the level at which fruiting fluctuates varies drastically from year-to-year.

4.2.2 Behavioral Data Collection and Estimated Daily Caloric Intake Calculation

We compiled full-day focal follows on nine Bornean orangutan mothers with dependent offspring following protocols from the Orang-utan Data Collection Standardization (<https://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html>; van Noordwijk et al., 2013). During each follow individual name, age class, focal activity, food item if applicable, height from ground, and associations with other individuals including distance between them were recorded in two-minute intervals. During this time, we also collected individual food items judged for close similarity in size and maturation as to those eaten by orangutans (Knott 1998) and sent them to Dr. Wartika R. Farida for macronutritional analysis at the Laboratorium Pengujian Nutrisi, LIPI-Bogor, Indonesia (see Chapter 3 for a more detailed description of the methodology). From these analyses, we were able to determine estimated daily caloric intake for a mother on a given day by pairing the nutritional information with the behavioral data for the given follow. While energetic biomarkers might be more strongly biologically correlated with the previous day's caloric intake, we used caloric intake of the same day as sample collection to

maximize sample size for the study as multiple samples were collected on the first day of observation.

4.2.3 Field Urine Collection and Ketone Analysis

We collected urine from the first void in the morning during focal follows, and we employed either of two methods to collect the urine: 1) spreading a clean plastic sheet beneath a urinating individual or catching the urine in a plastic bag on a stick, or 2) collecting the urine from forest vegetation (Knott, 1999; Table 4.1). Ketones can be quantified in the field using urinalysis strips (Chemstrip 10 UA, Roche Diagnostics) made for humans, which have been shown to detect ketones in orangutans (Knott 1998). Ketones were measured twice: once immediately after collection while still in the forest, and a second time after returning to the field station laboratory. To use urinalysis strips, 100µl of urine is pipetted onto the strip, and the result is compared with a corresponding color index. The measurement of ketone bodies follows a categorical valuing system: negative, positive, and double positive. This method has been validated in the laboratory with orangutan urine (Naumenko et al. In Revision, 2016). Additionally, after returning to the field station laboratory, we measured specific gravity using a handheld spectrometer (Atago PAL-10S) by pipetting 100µl of urine onto the lens and receiving an instantaneous reading. Once all field analyses were complete, we split samples into 200µl aliquots and froze them at -20°C in a solar freezer. Each sample was labeled with time, date, and individual. At the end of a field season, all urine samples were then transported back to the United States under the same storage conditions and stored at -80°C until analyzed at Rutgers University. Export permits were obtained with the assistance of our

Indonesian counterpart (UNAS) and we have maintained collection permits for urine samples since May 2012.

Table 4.1: Sample sizes of the project, divided by age of a mother's infant.

Infant Age Category	Cortisol	UCP	Urea	Ketones
<i>A. 0-6months</i>	37	30	27	75
<i>B. 6-12months</i>	21	27	20	44
<i>C. 12-18months</i>	36	32	26	64
<i>D. 18-24months</i>	21	23	7	51
<i>E. 24-36months</i>	16	21	18	85
<i>F. 36-48months</i>	28	35	30	107
<i>G. 48-60months</i>	43	38	44	99
<i>H. 60+months</i>	15	14	19	54
Total	217	220	191	579

4.2.4 Laboratory Urine Analysis

We performed all laboratory analyses in the Laboratory for Primate Dietary Ecology and Physiology at Rutgers University, under the supervision of Dr. Erin Vogel.

4.2.4.1 Cortisol

We assayed urinary cortisol using a commercial enzyme-linked immunoassay kit designed for analysis with urine, among other substrates (Arbor Assays, Ann Arbor, Michigan). For the complete procedure, please refer to the DetectX Cortisol Enzyme Immunoassay Kit protocol (<http://www.arborassays.com/documentation/inserts/K003-H.pdf>). We have validated this kit for use on orangutan urine using both recovery (recovery was 116%) and parallelism methods (Andreasson et al. 2015). Our starting sample dilution was 1:20, intra-assay CV for QC low was 11.82 and 9.99 for QC high, and inter-assay CV for QC low was 5.97 and 6.78 for QC high.

4.2.4.2 UCP

We assayed urinary C-peptide of insulin using a commercial radioimmunoassay kit designed for analysis with urine (EMD Millipore Corporation, St. Charles, Missouri) following the Millipore Human C-peptide RIA protocol, which has been validated on orangutan urine (http://www.emdmillipore.com/US/en/product/Human-C-Peptide-RIA,MM_NF-HCP-20K) (Emery Thompson and Knott 2008). Our starting sample dilution was 1:2, intra-assay CV for QC low was 5.35 and 4.77 for QC high, and inter-assay CV for QC low was 8.41 and 4.49 for QC high. We included samples with extremely low concentrations as long as the sample CV was below 20%, as these are biologically relevant data at or near a concentration of 0 pg/ml. We excluded two samples that were undetectable.

4.2.4.3 Urea

We assayed urinary urea using a commercial quantitative colorimetric determination kit designed for analysis with urine, among other substrates (BioAssay Systems, Hayward, California) following the QuantiChrom Urea Assay Kit protocol (<https://www.bioassaysys.com/Datasheet/DIUR.pdf>). While this kit was designed for use with all species, we have validated this kit for use on orangutan urine, as recovery was 94% and the urine pool was parallel to diluted standards (Andreasson et al. 2015). Our starting sample dilution was 1:20, intra-assay CV overall was 0.027 and our inter-assay CV for standard 1 was 7.61, standard 2 was 8.73, and standard 3 was 8.86.

4.2.4.4 Standardization

Cortisol, UCP, and urea assays we used produce raw concentrations (pg/ml for cortisol and UCP, mg/dl for urea), but any analysis of urinary metabolites must also consider the concentration of a urine sample, which can be affected by variables such as the time since the last urination and the level of hydration (Miller et al. 2004). Two of the most common methods for adjusting a metabolite's concentration to the concentration of urine are specific gravity correction (Osborne 1998, Anestis et al. 2009) and creatinine correction (Taussky 1954, Emery Thompson and Knott 2008). Specific gravity is a comparative measure between the density of a substance against the density of water, while creatinine is a byproduct of the breakdown of two compounds during muscle activity and is excreted at a theoretically constant rate in urine (Diskin 2007). However, creatinine excretion is highly variable between both individuals with different muscle mass and across populations (Boeniger et al. 1993). Therefore, we chose to use specific gravity to correct for the density of urine, using the following equation:

$$R * \frac{(P - 1)}{(S - 1)}$$

where R is the raw concentration for an indicator, P is the population average for specific gravity (for Tuanan, the value is 1.024), and S is the specific gravity of the sample.

4.2.5 Statistical Analysis

Since specific gravity values near the density of water can overinflate corrected results, we removed any values defined as outliers at least $3sd$ above the mean corrected concentrations for each physiological indicator. We constructed generalized additive mixed models (GAMMs) using the *mgcv* and *gamm4* packages in R statistical software

(Wood 2011, Wood and Scheipl 2017) to analyze the relationship between a mother orangutan's corrected physiological indicator concentration, infant age (in years), fruit availability (FAI), and the interaction between the two. All predictor variables were fitted with spline smoothers, interactions with tensor product smoothers, and orangutan ID as a random effect (random intercepts) to prevent pseudo-replication across individual follow days (Harrison et al. 2009). Models were fit using the Gaussian family with an identity link, and knots were selected to be spaced evenly across the axis using the minimal amount possible to avoid overfitting. We only analyzed first-morning voids to account for circadian rhythms in cortisol production (Koopmans et al. 2005). When the interaction term between FAI and infant age was significant, we further explored the relationship in two ways: 1) by visualizing the interaction plots, and 2) by constructing GAMMs with a factor-by-variable design. Alongside the dependent variable and infant age was a term splitting fruit availability by three categories based from FAI quartiles. The three categories used were Low (smallest 25% of FAI values, $FAI < 2.30\%$), Middle (middle 50% of FAI values, $FAI = 2.30\% - 5.90\%$), and High (largest 25% of FAI values, $FAI > 5.90\%$). This design allowed us to examine the relationship between the dependent variable and infant age during different periods of fruit availability within a single model. When reporting results, we refer to these models as factor-by-variable models. Additionally, we also constructed GAMMs that incorporated a mother's estimated daily caloric intake in addition to the previously mentioned variables, and compared model fit using both AIC and r^2 values. We included the interaction between FAI and daily caloric intake to incorporate the relationship seen between the two variables in mother orangutans (Chapter 3). GAMMS do not allow for the dependent

variable to be ordinal, meaning we had to construct alternate models for our ketone analysis. We chose to use cumulative link mixed models (CLMMs) using the *ordinal* package in R statistical software (Christensen 2019) because these regression models can account for random effects. In our ketone models, we added the number of consecutive low FAI months leading up to the month the sample was taken as another predictor variable.

4.3. Results

Overall, multiple indicators were significantly correlated with one or more of fruit availability, infant age, the interaction between fruit availability and infant age, or estimated daily caloric intake (Table 4.2).

Table 4.2: GAMM results for cortisol, UCP, and urea. Part B is the results for the models including estimated daily caloric intake.

A.	Cortisol (N = 217)			UCP (N = 220)			Urea (N = 191)		
<u>Model term</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
FAI	0.068	3.365	1.000	0.033	4.600	1.000	<0.0001	19.63	1.000
Infant Age	0.070	3.319	1.000	0.015	6.059	1.000	0.013	2.720	6.289
FAI*Infant Age	0.359	1.067	4.286	0.004	3.454	7.264	0.717	0.558	5.134
Time Collected	0.661	0.193	1.000	-	-	-	-	-	-
r ²	0.0398			0.0942			0.154		
	<u>p-val</u>	<u>F-stat</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
FAI	-	-	-	0.157	1.615	1.937	<0.0001	40.02	1.000
Infant Age - High FAI	-	-	-	0.066	3.424	1.000	<0.0001	6.566	5.674
Infant Age - Middle FAI	-	-	-	0.044	2.520	2.367	0.001	8.677	1.411
Infant Age - Low FAI	-	-	-	0.004	8.263	1.000	0.540	0.791	1.729
r ²				0.0833			0.114		
B.	Cortisol (N = 152)			UCP (N = 185)			Urea (N = 137)		
<u>Model term</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-value</u>	<u>F</u>	<u>df</u>	<u>p-value</u>	<u>F</u>	<u>df</u>
FAI	0.885	0.021	1.000	0.687	0.163	1.000	0.0002	14.99	1.000
Infant Age	0.577	0.313	1.000	0.001	10.56	1.000	0.182	1.879	1.058
FAI*Infant Age	0.440	0.600	1.000	0.048	2.084	6.459	0.707	0.118	1.006
Total Kilocalories	0.470	0.525	1.000	0.003	8.982	1.000	0.005	5.447	2.928
FAI*Total Kilocalories	0.044	0.339	2.868	0.222	0.000	1.000	0.991	0.060	3.233
Time Collected	0.168	1.921	1.000	-	-	-	-	-	-
r ²	0.0471			0.129			0.351		
AIC	3807.508			3580.539			2094.151		
	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>	<u>p-val</u>	<u>F</u>	<u>df</u>
FAI	-	-	-	0.002	9.541	1.000	-	-	-
Infant Age - High FAI	-	-	-	0.792	0.070	1.000	-	-	-
Infant Age - Middle FAI	-	-	-	0.012	3.430	2.812	-	-	-
Infant Age - Low FAI	-	-	-	0.001	12.30	1.000	-	-	-
Total Kilocalories	-	-	-	0.145	2.139	1.000	-	-	-
FAI*Total Kilocalories	-	-	-	0.180	1.814	1.000	-	-	-
r ²	-			0.171			-		
AIC	-			3573.88			-		

4.3.1 Cortisol

We analyzed 217 urine samples from nine mothers with infants estimated to be between newborns to 7.21 years old and FAIs between 0.572 – 10.052 ($\mu = 46874.63$ pg/ml, $\sigma = 55207.99$ pg/ml). We predicted a mother's cortisol concentrations would be highest during periods of low fruit availability (predictions 1 and 2) and while she had a young infant (prediction 3). Overall, a mother's cortisol was not significantly correlated to fruit availability, infant age, or the interaction between the two terms in the GAMM, not supporting any of our predictions. Of the 217 samples, 152 samples had corresponding estimated caloric intake for the day. After including daily caloric intake in the model, only the interaction between fruit availability and daily caloric intake was significant. This partially supports prediction 1, as a mother's cortisol levels were highest during periods of combined extreme low fruit availability and extremely low caloric intake (Figure 4.1).

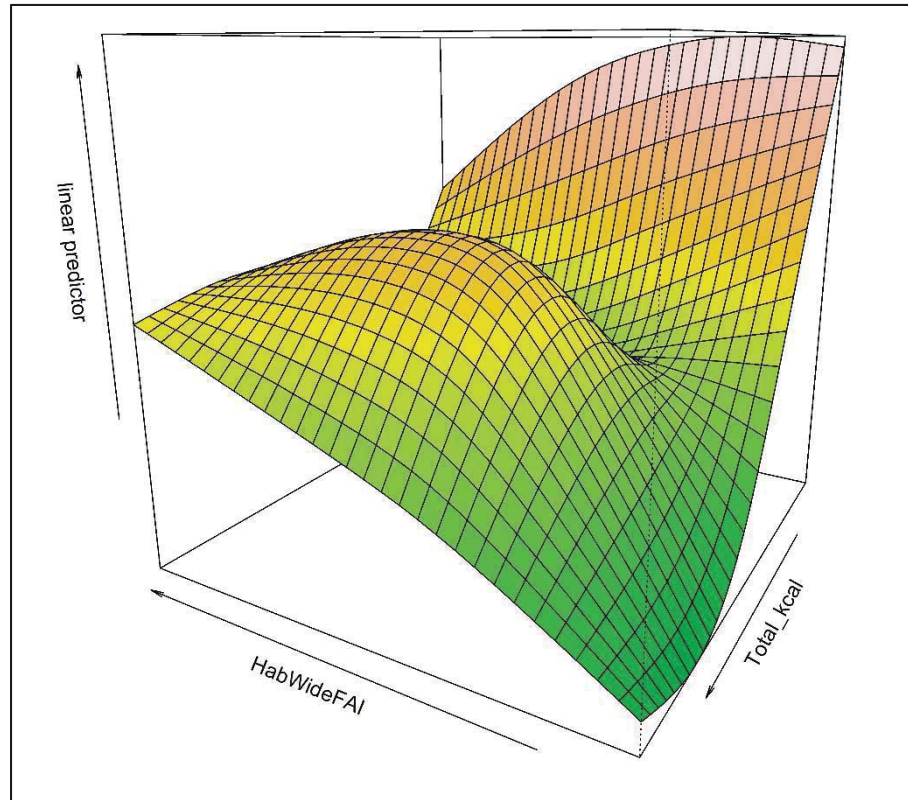


Figure 4.1: Contour plot of the interaction between the smoothing terms from interaction GAMM between a mother's cortisol concentration (linear predictor), fruit availability index, and estimated daily caloric intake (kcal).

4.3.2 Urinary C-peptide

For the UCP analysis, we used 220 urine samples from nine mothers with infants between newborns – 7.038 years old, and between FAI levels of 1.317 – 10.052 ($\mu = 3815.45$ pg/ml, $\sigma = 3921.80$ pg/ml). While only 185 of the 220 samples analyzed for UCP had corresponding daily caloric intake estimates, including caloric intake greatly increased the model fit. Therefore, we are only discussing results from the model with caloric intake, but have still reported the results from the original model (Table 4.2). We predicted that a mother's UCP concentrations would increase with fruit availability

(predictions 1 and 2), and her UCP levels would be lowest with a young infant, regardless of fruit availability (prediction 3). Both our predictions 1 and 2 were not supported, as both the interaction between infant age – fruit availability and caloric intake were significantly negatively correlated to UCP concentrations (Figure 4.2). Within the factor-by-variable model, fruit availability was also significantly negatively correlated to a mother's UCP concentrations. Our results support prediction 3 during low fruiting periods only, as infant age during these periods was significantly positively related to a mother's UCP concentrations. However, our prediction 3 was not supported during medium and high fruiting periods. During medium levels of fruit availability, a mother's UCP concentrations decreased until her infant was around 3.5 years old (Figure 4.3), and there was no significant change in a mother's UCP concentrations amongst infants during high fruit periods.

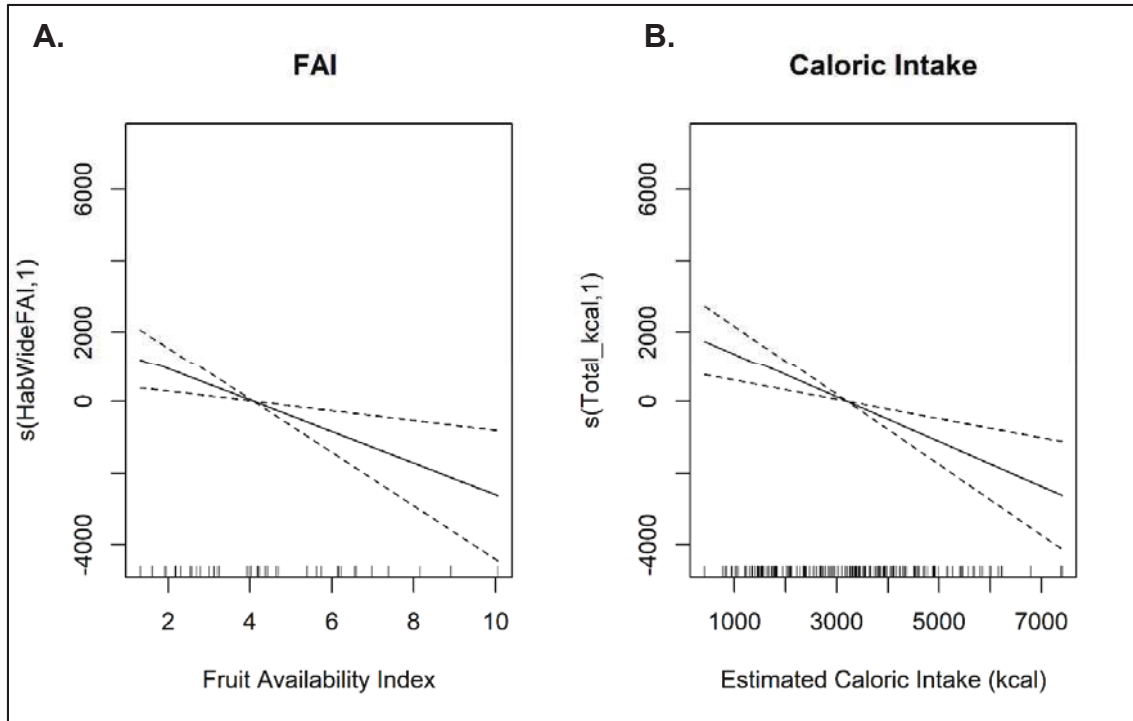


Figure 4.2: Smoothing terms from interaction GAMM between a mother's UCP concentration for a) fruit availability index and b) estimated daily caloric intake in mother orangutans, as seen in the model including estimated daily caloric intake.

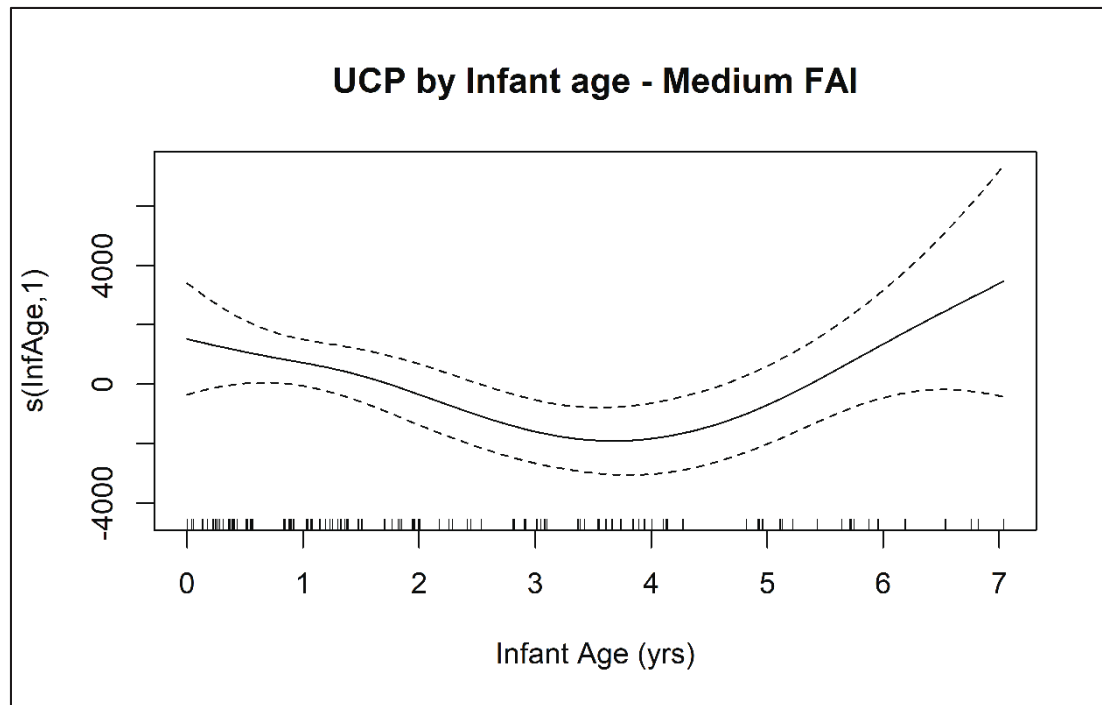


Figure 4.3: Relationship between the age of a mother's infant and UCP concentration in mother orangutans during medium fruiting periods, as seen in the factor-by-variable model including estimated daily caloric intake.

4.3.3 Urea

We analyzed urea levels in 194 urine samples from nine mothers with infants aged 0.001 – 7.211 years old and a FAI of 0.572 – 10.052 ($\mu = 690.29$ mg/dl, $\sigma = 687.30$ mg/dl), and 137 samples had corresponding daily caloric intake estimates. Including the estimates increased the fit of the model. We predicted that a mother's urea concentrations would decrease with both fruit availability and caloric intake (predictions 1 and 2), and her infant ages (prediction 3). Overall, we found support for all of our predictions. A mother's urea concentration significantly decreased as both fruit availability and caloric intake increases, regardless of the model used (predictions 1 and 2; Table 4.2; Figure

4.4). For caloric intake specifically, there was a sharp decline in her urea concentration from the maximum at 0 kcal to around 1,700 kcal, where it then stabilizes (Figure 4.4). The age of a mother's infant also had an inverse relationship with her urea concentration (prediction 3), and after exploring this in the factor-by-variable models, we found that there was a strong negative relationship between her urea concentration and infant age in the high and medium fruiting periods, but not the low periods. In the periods with the lowest fruit availability, a mother's urea concentrations did not vary significantly with the age of a mother's infant and are in fact overall higher.

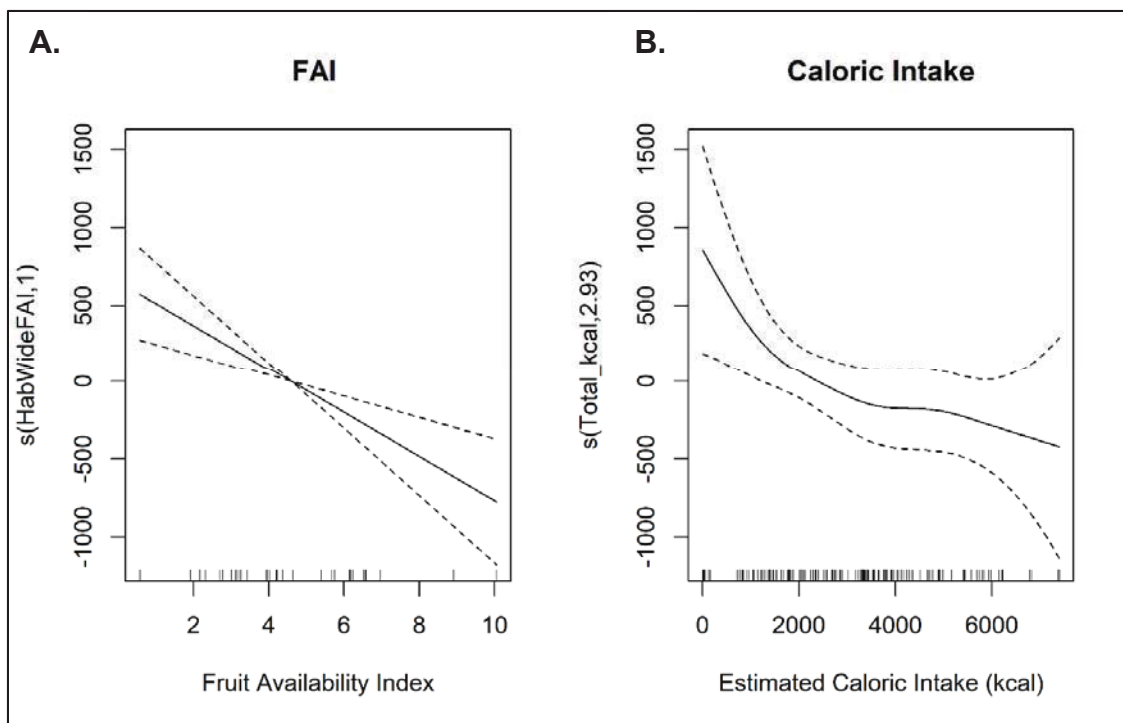


Figure 4.4: Smoothing terms from factor-by-variable GAMM between a mother's urea concentration and a) fruit availability index and b) estimated daily caloric intake in mother orangutans, as seen in the model including estimated daily caloric intake.

4.3.4 Ketone bodies

Because we were able to analyze ketones *in situ*, we were able to test 579 urine samples from twelve mothers with infants between 0 – 7.74 years old. The FAI for these samples ranged from 0.27 – 10.052. We predicted that a mother would have the highest likelihood of producing ketones in periods of fruit scarcity and when caloric intake was low (predictions 1 and 2), and when her infant is young (prediction 3). The interaction term between infant age and fruit availability was the only significant term in the CLMM (Table 4.3), meaning that the effect of infant age on a mother's ketone levels varied depending on how much fruit was in the environment. To investigate this interaction, we ran a multinomial log-linear model with the same model terms. Importantly, though, this model structure does not allow us to run orangutan ID as a random effect, which will have an effect on the model outcomes. The effect probabilities from the multinomial model show that, generally, a mother with a young infant in low fruiting periods has the highest probability of excreting ketones in her urine (Table 4.4), supporting all hypotheses. The probability of detecting ketones in her urine declines both as her infant ages and fruit availability increases, but the decline in probability is far greater as fruit availability increases. However, the pattern is slightly different between detecting probabilities for moderate levels of ketones and high levels of ketones. Whereas the probability for detecting moderate levels of ketones fits the pattern described above identically, the greatest probability for detecting high levels is in a mother with an older infant during the lowest fruit availability. Additionally, there is a general rise in high

level detection probabilities in mothers with new infants between FAI values of 0.3 – 5.

After this rise with fruit availability, though, there is an immediate drop-off to near zero.

Table 4.3: CLMM results for detection of ketone bodies a mother's urine.

	Overall (N = 579)			FAI High (N = 56)		
<u>Model term</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>
Fruit Availability Index	0.886	0.647	0.118	0.581	0.552	0.973
Infant Age	0.456	0.509	0.172	0.985	-0.019	2.587
# Previous Low FAI	0.057	-2.437	0.055	-	-	-
FAI*InfantAge	0.010	-2.437	0.055	0.889	-0.140	0.303
log-likelihood	-266.357			-7.86153		
AIC	546.714			25.723		
	incl. kcal (N = 318)			incl. kcal (N = 29)		
<u>Model term</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>
Fruit Availability Index	0.755	0.312	0.212	Cannot Fit		
Infant Age	0.196	1.294	0.268			
Total Kilocalories	0.065	-1.848	0.001			
# Previous Low FAI	0.251	-1.149	0.078			
FAI*Infant Age	0.020	-2.335	0.134			
FAI*Kilocalories	0.033	2.130	0.000			
Infant Age*Kilocalories	0.306	1.023	0.000			
log-likelihood	-146.285					
AIC	312.570					
	FAI Medium (N = 297)			FAI Low (N = 226)		
<u>Model term</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>
Fruit Availability Index	0.150	1.440	0.191	0.019	-2.348	0.269
Infant Age	<0.0001	-4.203	0.155	0.747	0.322	0.123
# Previous Low FAI	0.911	0.112	0.116	0.005	-2.793	0.059
log-likelihood	-107.308			-132.844		
AIC	226.615			277.688		
	incl. kcal (N = 152)			incl. kcal (N = 137)		
<u>Model term</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>	<u>p-value</u>	<u>z-score</u>	<u>se</u>
Fruit Availability Index	Cannot Fit			0.032	-2.149	0.719
Infant Age				0.728	0.347	0.236
Total Kilocalories				0.030	-2.174	0.001
# Previous Low FAI				0.592	-0.536	0.088
FAI*Kilocalories				0.095	1.671	0.000
Infant Age*Kilocalories				0.464	0.732	0.000
log-likelihood				-72.783		
AIC				163.563		

Table 4.4: Ketone production probabilities in a mother orangutan across fruit availability – infant age combinations from the multinomial log-linear model.

Infant Age*FAI effect (probability) for Negative						
		Fruit Availability Index				
		0.3	3	5	8	10
Infant Age (yrs)	Newborn	0.780504	0.746952	0.709701	0.628882	0.557733
	2	0.762532	0.845021	0.889742	0.935591	0.955538
	4	0.738502	0.908348	0.959631	0.988062	0.994612
	6	0.70711	0.946677	0.984725	0.997415	0.999183
	8	0.66724	0.969132	0.994017	0.999408	0.99987
Infant Age*FAI effect (probability) for Moderate						
		Fruit Availability Index				
		0.3	3	5	8	10
Infant Age (yrs)	Newborn	0.158129	0.149749	0.141177	0.123647	0.108807
	2	0.153636	0.101416	0.072752	0.04302	0.029934
	4	0.147974	0.065262	0.032253	0.010625	0.005003
	6	0.140902	0.040718	0.013604	0.002508	0.000807
	8	0.132224	0.024954	0.005645	0.000588	0.00013
Infant Age*FAI effect (probability) for High						
		Fruit Availability Index				
		0.3	3	5	8	10
Infant Age (yrs)	Newborn	0.061368	0.103299	0.149122	2.47E-01	3.33E-01
	2	0.083832	0.053562	0.037506	2.14E-02	1.45E-02
	4	0.113524	0.026389	0.008115	1.31E-03	3.85E-04
	6	0.151988	0.012606	0.001671	7.70E-05	9.82E-06
	8	0.200535	0.005915	0.000338	4.48E-06	2.50E-07

We were also able to include a mother's daily caloric intake estimate in 318 of the 579 samples, which increased the model fit (Table 4.3). Once a mother's caloric intake was included in the CLMM model, fruit availability, infant age, and the interaction between the two were all significantly related to a mother's ketone production. Again, we ran a multinomial log-linear model with the same model terms to investigate these relationships. At the lowest fruit availability, the probability of a mother producing

ketones increases as her infant ages. Conversely, at the highest fruit availability, a mother's probability of producing ketones is greatest when she has a young infant (Figure 4.5).

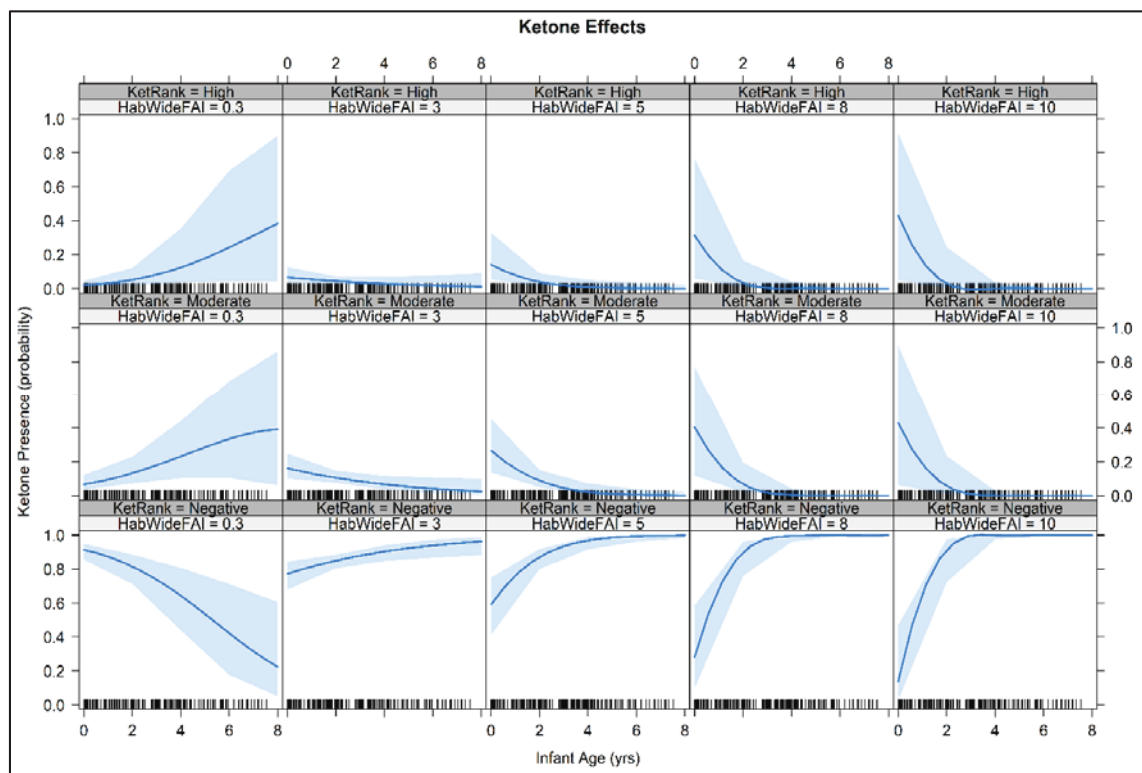


Figure 4.5: Probabilities of a mother producing ketones amongst fruit availability – infant age combinations, once estimated daily caloric intake is included in the model.

In an attempt to replicate the factor-by-variable models used for the other biomarkers, we ran the same models on data divided between low, medium, and high fruiting periods, but the high fruit period did not have enough samples to fit the model properly. During medium fruiting periods ($n = 152$), a mother had a significantly higher probability of producing ketones with younger infants (Figure 4.6). During low fruiting

periods ($n = 137$) however, fruit availability and a mother's total caloric intake, not the age of her infant, was significantly correlated to ketone production (Figure 4.7). Here, a mother's probability was highest when she consumed fewer calories. The number of months with low fruit availability leading up to the urine sample significantly impacted the likelihood of a mother's ketone production during low fruiting periods, where ketone production likelihood decreased with more low months leading up to collection.

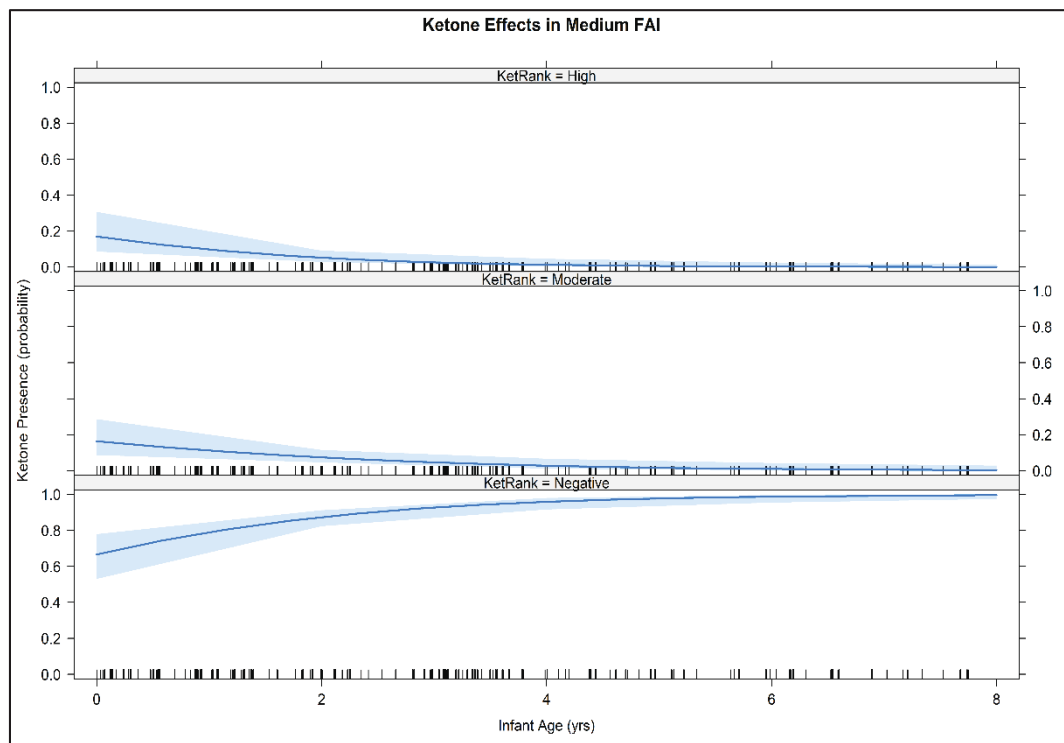


Figure 4.6: The relationship between infant age and ketone presence in a mother's urine during medium fruit periods.

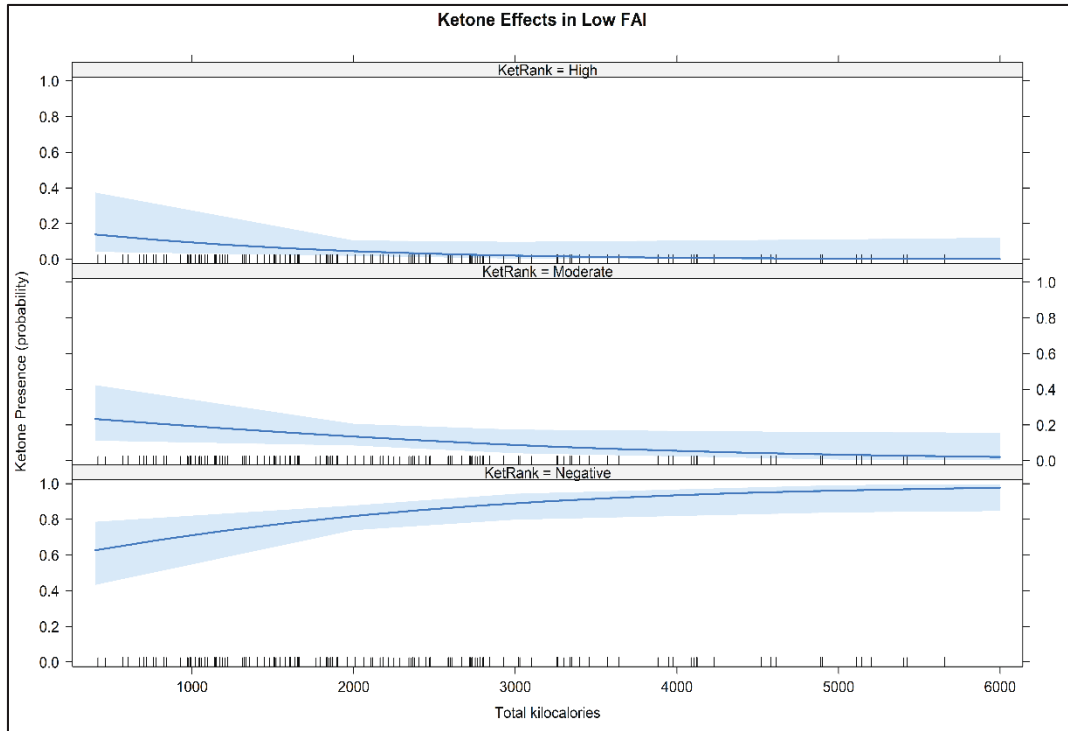


Figure 4.7: The relationship between total daily caloric intake and ketone presence in a mother's urine during low fruit periods.

4.4. Discussion

4.4.1 Cortisol

We only found support for variation in a mother's cortisol levels due to periods of extreme food shortage. Previous research speaks to the difficulty of using cortisol as an indicator of energetic condition. Physical stressors that have influenced primate cortisol levels not only include food availability and acquisition, but also exposure to pathogens, predatory threats, and interactions among other members of the population (Abbott et al. 2003). Additionally, the stress response system is equally impacted from beneficial inputs as much as challenges to the system (Pollard 1995). Together this means we can conclude little, if anything, about the effect of infant age on a mother's cortisol levels. Sample size

is a potential issue, as repeated long-term sampling is needed to ensure all physical and psychological contexts are captured within the umbrella of energetic fluctuations (Emery Thompson 2017). In addition to increasing sample size, future studies must include at minimum social variables to understand the fluctuations of cortisol levels across motherhood, as seen in wild chimpanzees (Emery Thompson et al. 2010) and mantled howler monkeys (Dias et al. 2017).

4.4.2 Urinary C-Peptide

A mother's UCP levels were highest during periods of moderate fruiting, but decreased as fruit availability rose, not supporting our prediction that UCP would be highest when the most fruit is available. There are at least two explanations for this relationship. First, it is possible that UCP in this instance is not as good of an indicator as previously thought, but this would go against both previous research in both a controlled, captive setting (Deschner et al. 2008, Girard-Buttoz et al. 2011) and a field setting (Sherry and Ellison 2007, Emery Thompson and Knott 2008, Grueter et al. 2014). Alternatively, it potentially is indicative of a mother's foraging behavior during high fruit periods and, as Emery Thompson (2017) notes is possible, that she is experiencing high energy status while having a low energy balance. A mother travels farther and more often during periods of high fruit availability, searching for ripe fruit, and therefore expending more energy in an attempt to maximize nutritional intake (Chapter 2). In fact, ripe fruit is found significantly more in a mother orangutan's diet during high fruit periods (Chapter 2, Chapter 3). Still, even though she is consuming more calories, the energy expended during traveling could be potentially high enough to lower her overall energy balance. A

mother can potentially build fat reserves, increasing her weight and making locomotion energetically more expensive. Additionally, macronutrient selection and intake plays an important role in food choice (Simpson et al. 2004, Felton et al. 2009a, Rothman et al. 2011). Lower levels of UCP during high fruiting periods might indicate a mother is increasing energy expenditure because it is possible to better select foods that correspond with macronutritional requirements, instead of just maximizing energy. Unfortunately, high fruiting periods are becoming rarer at Tuanan, and consequently high fruit periods are the least sampled period in this study. Hopefully, future research at this site or other sites can further elucidate the relationship seen between higher fruit consumption, greater daily path lengths, and lower UCP concentrations.

The positive relationship between a mother's UCP levels and age of her infant during low fruit periods indicates a mother is consistently less behaviorally constrained by her infant and partially supports our prediction that UCP concentrations would be lowest with young infants. This is similar to what is seen in mantled howler monkeys, in which mothers with young infants have their lowest UCP values but highest levels of vigilance and infant carrying (Dias et al. 2018). However, the nadir in an orangutan mother's UCP levels with infants between three and four years old in medium periods of fruit availability does not support our above prediction. Around this age, infants are travelling much more independently (van Noordwijk et al. 2009) and can process more foods in the environment (Schuppli et al. 2016), but are still relative novices at both independent travel and foraging. Still, milk is a significant part of an orangutan infant's diet at three years old (van Noordwijk et al. 2013), so a mother is still paying the energetic cost of milk production in addition to behaviors like infant carrying (albeit at

much lower levels). Since ripe fruit is intermittently available compared to high periods of fruit availability, a mother orangutan is potentially inhibited by her increase in time spent searching for fruit, which appears to lead to a more negative energy balance. An orangutan infant learns to process the foods in the environment from her mother (Jaeggi et al. 2008, Schuppli et al. 2016). It is possible that a mother's negative energy balance during periods when more food items are available is a consequence of the extended nursing period, where for multiple years an infant orangutan learns to navigate the habitat, process food, and forage efficiently from her mother. Overall, a mother's UCP levels seemingly provide evidence that a mother orangutan shifts her energetic strategy depending on both her infant's age and the availability of fruit in the environment, as seen in Chapter's 2 and 3.

4.4.3 Urea

Our results seem to contradict the accepted model of nitrogen balance in vertebrates (see Martinez del Rio and Wolf, 2005). Nevertheless, our results do make sense in light of what we know about the variation in activity, foraging behavior, and diet of mother orangutans at Tuanan (Vogel, *et al.*, in prep), and support our prediction that a mother's urea would be dependent on how much energy she is utilizing from dietary protein. During low fruit periods, a mother spends significantly more time foraging on leaves than during high fruit periods (Chapter 2) and ingests significantly more available protein while she has an older infant (Chapter 3). Similarly, during low fruit periods a mother with a younger infant consumes significantly fewer calories (Chapter 3). Together, these results seem to explain why we see greater urea excretion from a mother

during periods of lower fruit availability, and within periods of low fruit availability we see greater urea excretion with a lower daily caloric intake, instead of a relationship with infant age. However, previous research has demonstrated that only a small percentage of dietary protein (8% in humans) is actually used to produce glucose through gluconeogenesis and consequently the production of urea (Fromentin et al. 2013). Low energy intake increases the amount of degraded body proteins that are catabolized for gluconeogenesis (Barboza and Parker 2006), and during high protein diets, gluconeogenesis increases to compensate for the lack of glycogen stores (Veldhorst et al. 2009). Multiple capital breeders, or species that rely on energy stores to fuel reproduction, encounter a dearth in nitrogen availability while lactating and consequently rely on body protein to maintain their production of milk (Barboza and Parker 2008, Taillon et al. 2013, Borrell et al. 2016). A mother orangutan, which is neither a traditional capital or income breeder (species that rely exclusively on food intake to fuel reproduction), seemingly fits this same pattern, even though she consumes greater amounts of dietary protein. During periods of high fruit availability, however, a mother has enough glycogen stores available and has reduced gluconeogenesis from body protein. Hence, she excretes lower levels of urea in her urine.

4.4.4 Ketone Bodies

While fruit availability overall was significantly related to detection of ketones in a mother's urine, supporting our hypotheses, infant age and a mother's estimated daily caloric intake affected ketone detection differently depending on the availability of fruit in the environment. During low fruiting periods, only total caloric intake was

significantly related to a mother's ketone production. Her caloric intake is lower during periods of low fruit availability (though mothers with older infants do consume similar caloric amounts as mothers in higher fruit periods; Chapter 3), and a mother is potentially more at risk of not meeting her daily caloric needs regardless of her infant's age. Hence, a mother has a greater chance of producing ketones when she catabolizes her body fat reserves to compensate for the lack of calorically rich food in the environment (e.g., lower daily caloric intake). During low fruiting periods, a mother is in general more likely to produce ketones, regardless of her infant's age. However, the fact that a mother is less likely to produce ketones in longer prolonged periods of low fruit availability suggests that her fat stores are finite and not being replenished. In medium fruit periods, however, infant age was the only significantly correlated factor to the presence of ketone bodies in a mother's urine. Preferred foods that are calorically rich are more readily available, so a mother's behavior related to rearing an infant becomes a more important factor in determining her caloric intake. Therefore, when she has a younger infant (less than three years old), she catabolizes her fat stores in order to meet her energetic demands.

4.4.5 Synthesis and Conclusion

In summary, this study provides evidence that a mother orangutan experiences variation in both her energy balance and status across the lactation period, albeit sometimes in directions we did not predict (Table 4.5).

Table 4.5: Summary of biomarker results

Biomarker	Variables		
	Fruit Availability	Infant Age	Estimated Caloric Intake
Cortisol $\mu = 46874.63 \text{ pg/ml}$ $\sigma = 55207.99 \text{ pg/ml}$	No effect	No effect	No effect
UCP $\mu = 3815.45 \text{ pg/ml}$ $\sigma = 3921.80 \text{ pg/ml}$	Decreased during high fruit periods	Nadir with infant age around 3.5 years old in medium fruiting, Positive relationship with infant age in low fruiting	Inverse relationship
Urea $\mu = 690.29 \text{ pg/ml}$ $\sigma = 687.30 \text{ pg/ml}$	Inverse relationship	No effect	Inverse relationship
Ketones	Highest probability with low fruiting, largest variation	Probability increases with infant age in low fruiting, decreases with infant age in medium and high fruit periods	Highest probability during low fruiting with low caloric intake

In general, the period where a mother has the worst energetic condition is while she has a young infant in low periods of fruit availability. Especially environmentally stressful periods can lead to a mother catabolizing both fat (ketones) and protein (urea), while having a negative energy balance (UCP). Still, as noted as a distinct possibility by Emery Thompson (2017), a mother can also experience simultaneously high energy status and low energy balance, as seen around high fruit periods. In fact, Emery Thompson (2017) points out that this is most common in individuals living in seasonal habitats. Orangutans in peat-swamp forests live in an unpredictably seasonal environment (Vogel et al. 2015). Within this unpredictable seasonality, mothers are raising infants that present continually different behavioral and physical challenges, varying the balance of parental care (Trivers

1972, Clutton-Brock 1991). Combining multiple physiological indicators of energetic condition give us a glimpse of how a mother is affected by these changes in ways that a single biomarker couldn't explain, such as a mother's high energy status but low energy balance during high fruiting periods. Bringing together noninvasive *in situ* and laboratory methods allows us to study a species that is difficult to monitor continuously, and provides us with a more holistic picture of their ecology and evolution.

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Chapter 5. Conclusion

5.1 Summary

Mammalian motherhood takes many forms, and orangutan motherhood is one of variable environments (Marshall et al. 2009, Vogel et al. 2012b, 2017) and constant teaching (Van Noordwijk and Van Schaik 2005, Jaeggi et al. 2008, 2010, Schuppli et al. 2016) by oneself across multiple years (van Noordwijk et al. 2013b, 2018). Lactation is an extremely costly period for mothers (Ofstedal 1985, Gittleman and Thompson 1988), and primate mothers utilize a variety of strategies to navigate this period, including varying their activity and behavior (Dunbar and Dunbar 1988, Lappan 2009, Dias et al. 2011), and increasing the amount of calories they consume (Matsumoto-Oda and Oda 2001, McCabe and Fedigan 2007, Murray et al. 2009, Ruivo et al. 2017). Mother orangutans have the longest lactation period of any mammal (van Noordwijk et al. 2013b, 2018), but still there is relatively little research (apart from what is cited here) on what strategies an orangutan mother uses to ensure infant survival and maximize fitness. In this dissertation, I address this dearth of knowledge, bringing in multiple lines of evidence to better understand how a mother orangutan operates, what influences her behavior, and what exactly taxes her energetically and nutritionally throughout lactation.

In Chapter Two of this dissertation, I focused my investigation on the behavior and general diet of an orangutan mother. I aimed to understand how these two variables vary with the age of her infant across fruiting periods of different magnitudes and consequently if there are key periods of behavioral variation that can be elucidated within the entire lactational period. I found that orangutan mothers seemingly use two different strategies to forage, depending on how much fruit is in the environment. When fruit

availability is high, a mother orangutan will seek to maximize her energy and nutrition. While she has a young infant, she is not able to travel as freely between patches of food and therefore increases her active period to forage on as much ripe fruit as possible. Once her infant ages and learns how to navigate the environment, a mother can then potentially seek out high quality ripe fruit across a greater area. She travels more throughout the day over greater distances, feeding less than when she has a young infant. During periods of low fruit availability, however, a mother minimizes her activity in order to conserve energy. A mother feeds much less on fruit and overall is active much less than during periods of greater fruit availability. Additionally, from these results, I was able to understand that a mother orangutan's period of maximum maternal cost, which includes time, energy, and behaviors needed to improve an infant's chances of survival (Trivers 1972, Clutton-Brock 1991), is when her infant is around two years old. Regardless of how much fruit is available in the habitat, a mother alters her behavior more than during other times in the lactational period. Other evidence from previous research supports this, as a two-year-old infant orangutan still requires their mother for travel (van Noordwijk et al. 2009, Chappell et al. 2015) and has yet to develop enough competence to feed primarily on solid food (Jaeggi et al. 2010, van Noordwijk et al. 2013b, Schuppli et al. 2016).

Chapter Three takes the approach I used in Chapter Two and applies it to a mother's estimated intake of calories and macronutrients. I sought to understand how a mother's intake varies with both the age of her nursing infant and the amount of fruit in the habitat. Additionally, I applied the Geometric Framework of Nutrition (Simpson et al. 1993) to understand if a mother's foraging behavior is focused on the relative amounts of

macronutrients in her diet. I found that when she has a young infant, a mother's caloric intake depends significantly on the amount of fruit in the habitat. During high fruit periods, her caloric intake increases, but during low fruit periods, it decreases substantially. Additionally, during these low periods, a mother's carbohydrate intake drops when her infant is around two years old, something not seen in mother orangutans during periods of greater fruit availability. This result supports what I found in Chapter Two, where a mother's fruit consumption is much less during the same period, and further suggests that the period of maximum maternal care is when a mother has a two-year-old infant. By applying the Geometric Framework of Nutrition, I was able to determine that in high fruiting periods, a mother has a remarkably stable macronutrient intake ratio regardless of her infant's age. As the amount of fruit decreases in the environment, her ratio becomes much more variable with infant age, including surpassing the ratio found during high fruit availability. Orangutans are the only wild non-human primate that builds fat reserves which they then use later (Knott 1998, Harrison et al. 2010). This result supports the idea that a mother orangutan targets specific foods when she is able in order to build fat reserves for future challenging energetic periods.

In Chapter Four, I analyze urinary biomarkers to understand how a mother's energetic condition varies with the age of her infant and the availability of fruit in the environment. I bring together evidence from urinary cortisol, which potentially gives us insight into whether a mother is experiencing energetic stress (van Schaik et al. 1991, Saplosky 1992), C-peptide of insulin, an indicator of energy balance (Sherry and Ellison 2007, Emery Thompson and Knott 2008), urea, which indicates if an individual is catabolizing nitrogen in her body (Barboza and Parker 2006, Vogel et al. 2012b), and

ketone bodies, an indicator of fat catabolism from body stores (Knott 1998, Harrison et al. 2010). Collectively, these four indicators provide evidence that support my conclusions from Chapter Two and Chapter Three, that a mother orangutan's worst energetic condition is while she has a young infant in periods of low fruit availability. Cortisol and urinary C-peptide can both provide information about a mother's energetic balance, or the difference between energy intake and expenditure. While the cortisol results were difficult to interpret, I did find that a mother's greatest period of energetic stress was during periods of extreme fruit shortage, regardless of the age of her infant. Surprisingly, I found that a mother's C-peptide levels were highest in periods of low fruit availability. This makes sense in light of my Chapter Two conclusion that a mother is minimizing activity during these periods, which would in turn raise her energy balance. However, her UCP levels were also lower when she had a young infant. I inferred a mother's energy status, or the amount of stored energy available, by analyzing her urea and ketone body levels. A mother's urea levels were highest in periods of low fruit availability, and a mother's greatest likelihood of producing ketone bodies was when she had a young infant during periods of low fruit availability. Collectively, I showed that a mother is most constrained energetically during periods of low fruit availability when she has a young infant, even though her energy balance was lowest during periods of high fruit availability.

5.2 Unifying and Applying Findings

Each chapter of this dissertation provides foundational information for understanding what it is like to be a mother orangutan lactating in a peat-swamp forest.

The chapters are united under the umbrella of the energetics of motherhood, and collectively provide a picture of what behaviors a mother orangutan exhibits, when she exhibits them, and why she exhibits them. During periods of high fruit availability, mothers are able to maintain a constant energetic balance, macronutrient ratio, and potentially build fat reserves regardless of her infant's age. The large amount of preferred food in the habitat lets her potentially select food items that meet her energetic and nutritional requirements as these change with the needs and capabilities of her infant. For instance, a mother will feed on the less abundant but calorie-rich ripe fruit with a young infant but shift to the more abundant less ripe fruit with older infants. Older infants can process more complex foods while also requiring more solid food intake (van Noordwijk et al. 2013b, Schuppli et al. 2016). She makes this transition without varying her feeding time, increasing her calorie intake, and maintaining her macronutrient balance. This isn't possible when there is little fruit in the environment and a mother must rely on non-preferred food items. A mother cannot maximize her energy intake when her infant is most costly and must utilize another strategy. There are periods where a mother must rest significantly more and rely on less-calorically rich foods, like leaves and bark. Perhaps the most challenging time for a mother is while she has an infant around two years old in a period of low fruit availability. Her infant still requires much help with locomotion and cannot process much of the food in the environment (van Noordwijk et al. 2009, Chappell et al. 2015, Schuppli et al. 2016), which impacts her energetic condition. A mother with an infant in this most costly period has a lower energy balance and is much more likely to utilize her fat reserves. She cannot maintain her caloric intake and she shows much more variation in her macronutrient ratio. To make it through this challenging time, a mother

reduces her activity and minimizes her energy expenditure, allowing her to exist in a low energetic condition. She cannot utilize the same strategy as during a high fruit period because her energy requirements would be too high, potentially killing her and/or her infant.

Most primate mothers, including humans and other great apes, live in much more energetically-rich and/or predictably seasonal environments than orangutans (Brockman and van Schaik 2005). Like orangutans, many primates, characterized by their extended life histories and periods of development (Harvey and Clutton-Brock 1985), cannot rely on a single predictable season to complete a reproductive cycle from birth to complete independence from the mother (Emery Thompson 2013a). However, mothers can utilize seasonality to support the costliest periods of motherhood in order to maximize reproductive success and fitness (Brockman and van Schaik 2005, van Noordwijk 2012, van Noordwijk et al. 2013a). Species like chimpanzees, who have extended lactation periods that span over multiple seasons, also live predominately in environments where high preferred food abundance allows for larger average group sizes and gregarious social structures (Sterck et al. 1997). Alloparenting provided by conspecifics reduces the costs associated with lactation and allows a mother to maintain a higher energetic condition (Emery Thompson et al. 2010, Bădescu et al. 2016, Raboin 2018). Human mothers rely significantly on others to reduce the energetic costs associated with a lactating mother (Kaplan et al. 2000). Orangutan mothers are not able to fall back on conspecifics to help reduce the energetic taxation of a costly infant and therefore occupy one end of the spectrum defined primate maternal strategies; since orangutan motherhood is unique among primates, it is perhaps one of the best comparators to use when describe

other strategies of motherhood. Whereas other primate mothers fail when presented with a severe energetic challenge (Lee and Hauser 1998, Gould et al. 2003), mother orangutans shift their strategy to ensure infant survival (van Noordwijk et al. 2018). The ability to adapt behaviorally to changing foraging conditions in conjunction with offspring need ensures a mother can maintain her energetic condition across offspring dependence. This is especially important as a mother's condition is the most important factor in determining when she is likely to reproduce again (Brockman and van Schaik 2005, Emery Thompson 2013a). Orangutan motherhood, as described in this dissertation, could also be a potential tool when investigating the evolution of hominin mothers. Early *Homo*, like orangutans, lived in marginal energetic habitats, but have over time developed an alternate strategy to overcoming challenging periods during lactation (O'Connell et al. 1999). It is possible that the strategies we see in orangutans give insight into the strategies used before *Homo*'s reliance on conspecifics (van Noordwijk et al. 2013a).

5.3 Future Work

This dissertation was the beginning in bringing together multiple lines of evidence to understand what the influential variables are for a mother orangutan's activity, feeding behavior, and energetic condition throughout lactation. Each chapter approached the question from a different perspective, and future research should first consolidate the important information to better understand questions that arose from this thesis. Specifically, future research should 1) investigate the relationship between macronutrient ratio and the building of fat stores, 2) seek to understand the relationship between daily

path length and urinary C-peptide levels, and 3) provide a more in depth look at the relationship between caloric intake and all of the biomarkers included in Chapter Four. Additionally, as mentioned in the introduction, orangutans live in a variety of habitats, and each habitat has specific characteristics (Husson et al. 2009, Marshall et al. 2009). If anything, this project demonstrated that wild orangutan mothers respond behaviorally and energetically to their environment, and must use multiple strategies to raise an infant successfully in a peat-swamp forest on Borneo. However, other habitats might influence orangutan mothers differently, especially those with higher degrees of sociality (Singleton and Van Schaik 2001). It is also possible, and highly likely, that specific food species-item combinations have a great influence on mother orangutans, including non-fruit items. Future studies should evaluate the relationship between a mother's food preference, food availability, behavior, and energetics. Finally, this study did not look at the influence of gestation in any way. It is possible that mother orangutans used in this analysis were pregnant while they have older infants, and that this in turn would influence her energetics and behavior. Future studies should focus on this transition from lactation to gestation and investigate how this translates to weaning and conflict between a mother and her older infant.

While researching wild orangutans, I routinely encountered sample size issues, most of which were an artifact of my ability to either 1) follow a specific mother with an infant of a particular age, or 2) the ability to collect, transport, and analyze a small amount of urine. It is highly unlikely that any dissertation research project will focus on orangutan motherhood can be conducted longitudinally, as there are time and funding limits that every graduate student encounters, hence why this project was cross-sectional.

Continuing this research at Tuanan outside of graduate school in a longitudinal fashion, when long-term data collection can improve sample size, will hopefully fine-tune or correct the conclusions I have put forth here.

5.4 Conclusion

In summary, this dissertation provides evidence from multiple methodologies that the energetics and feeding behavior of a mother orangutan is influenced by the combination of the age of her infant and the amount of fruit in the habitat. An orangutan mother must be flexible as she is bound to encounter periods of preferred food shortage and energy deficits across her multiple years of lactation. While many primate studies collectively group lactating mothers into a single category, there are potential significant differences that can occur depending on the age of infants and the availability of food in the habitat. While orangutans might be the most extreme case of encountering a variety of circumstances across lactation, other studies must also consider the impact from these variables.

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