Meat Consumption in Omnivorous-frugivorous Primates across Continents: a comparative analysis

by

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Abstract

Primate dietary choices are subject to changing environmental conditions. Therefore, all primates must display varying degrees of behavioural plasticity and adaptability to ecological pressures and modify their diets in response to low food availability. Currently, primates worldwide are threatened by increasing deforestation and the removal of crucial food sources via anthropomorphic activity. Omnivorous-frugivorous primates in particular exhibit extreme degrees of behavioural and dietary plasticity in the wake of resource scarcity but generally do not include considerable portions of meat in their diets. Therefore, an increase in the amount of meat eaten (however small) could be an indicator of dietary stress due to habitat degradation. Considering the increasing fragmentation of primate habitats I investigated the relationship between primate meat consumption and food loss. The diets of a number of omni-frugivore primate species inhabiting different geographic regions, habitat types, and continents, were compared to determine variability in the percentage of meat consumption between each group and whether primate meat intake rose in tandem with deforestation over time. Omni-frugivores in drier habitats or regions of marked seasonality consumed more meat than those found in wetter regions. There was no relationship between the protein content of the plants ingested and meat intake. Furthermore, the percentage of meat in the diets of omni-frugivores tended to increase with the rate of habitat fragmentation, with the average percentage of meat consumption rising by 1.1% between 1970-2015. The relationship between increasing meat consumption and deforestation may significantly aide the conservation of forests, crucial plant food items and sustainability of primate population persistence and health.

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CHAPTER 1: INTRODUCTION

1.1.1 THESIS OBJECTIVES

In this thesis, I investigate the relationship between ecology and the percentage of meat in omnivore and frugivore diets. Since meat consumption is highly variable across primate species I conducted my research to see if this variability is connected with a primate's environment. My second objective is to evaluate if the percentage of meat in the diets of omnivorous and frugivorous primates has changed in tandem with extensive anthropogenic deforestation over the past 45 years (1970-2015). Since 1970, industrial logging has caused an increase in the rate of deforestation worldwide (Oates et al., 2013). Primates consuming such a rare food item at an elevated rate might indicate a loss of preferred and alternative resources within their habitats. I focus on primates that have the ability to consume meat, yet only consume small portions of it. Folivores will not be considered, as the amount of meat they consume is negligible, and there are not enough data to adequately assess primates exhibiting this diet specialization. I am not including insectivores since they already consume a substantial amount of meat and could therefore bias my results (see chapter two for details).

My research could contribute to primate conservation efforts by adding another variable, increased meat consumption, as an outcome of marked changes in primate diets due to human expansion. The global perspective of my study may help pinpoint where a change in meat consumption is particularly extensive. By doing so, my investigation could highlight which geographic regions are so heavily deforested that primates must resort to increasing their meat intake to avoid starvation. These areas could then be targeted for increased conservation measures. Considering that meat is such a rarely consumed food item, understanding the ecological relationship between primates and meat consumption can help conservationists understand primate habitat requirements. Additionally, my research may help increase awareness of predator-prey interactions. Increased meat consumption by primates could potentially affect the ecosystem if they are over-hunting prey. Below I present background information relevant to the above research project.

1.1.2 A BRIEF HISTORY OF PRIMATE EVOLUTION

The ancestors of modern primates (Euprimates) appeared 50-55 million years ago (MYA) at the start of the Eocene (55-33 MYA), in a climate much warmer than North American and European climates today (Fleagle, 2013). Average daily temperatures reached 30° Celsius and tropical and sub-tropical forests covered the world, which facilitated the radiation of flowering plants (Erikkson, 2014). Early primates flourished under these conditions and filled the seed-disperser niche in North America, Africa, and Eurasia (Gingerich, 2012; Sussman, 2013). Primates were able to spread globally during the Eocene due to the lack of polar ice and the presence of land bridges (Gingerich, 2012).

Strepsirrhines and Haplorhines diverged soon after the appearance of Euprimates (Gingerich, 2012). Strepsirrhini is a suborder comprised of extant lemuriforms, galagos and lorisiiforms while Haplorhini encompasses Apes as well as old and New World monkeys (Fleagle, 2013). Paleoanthropologists have uncovered the oldest fossils thus far of tooth-combed strepsirrhines, which date from 41-37 MYA, in Africa (Fleagle and Gilbert, 2013). The earliest haplorhine-like fossils, referred to as Omomyiforms and discovered in Asia, date to 45 MYA (Fleagle and Gilbert, 2013). These primates were similar to extant tarsiers (*Tarsiidae)* with a rounded skull, large eyes and tarsier-like limbs for leaping (Cartmill and Smith, 2011). They also had morphologically primitive traits such as bony ear canals and large gaps between the upper incisors (Cartmill and Smith, 2011). The Earth's temperatures dropped and environments changed from tropical to temperate forests at the end of the Eocene (33 MYA)(Fleagle, 2013). The sea level lowered as a result of glaciation at the Earth's poles and continents moved towards present-day alignments (Fleagle, 2013). The cooler temperatures at the end of the Eocene resulted in a mass mammalian extinction event and led to the extinction of North American primates (Gingerich, 2012;Fleagle, 2013).

By the Oligocene (33-21 MYA) haplorhines were the dominant primates in Africa and diverged into two groups: catarrhines (Old world Monkeys and Apes) and platyrrhines (New World monkeys) around 33 MYA (Fleagle and Gilbert, 2013). Extant platyrrhines live in South America while catarrhines live in Africa and Asia (Ganzhorn et al., 2009; Fleagle, 2013). Primatologists posit that platyrrhines reached South America by rafting (Perez et al. 2013). The Atlantic Ocean's currents and the lowered sea level allowed the platyrrhines to cross the Atlantic by floating from island to island on natural vegetative rafts (Perez et al. 2013). The oldest platyrrhine fossils, which have primitive skeletons but exhibit extant platyrrhine dentition, are from South America and date to 25 MYA (Godinot, 2015). By the Oligocene's end, cercopithecoids (Old World monkeys) were abundant in Africa and possibly diverged with hominoids 25 MYA (Stevens et al. 2013).

Eurasia, Africa, and Madagascar became warmer in the Miocene (23-5 MYA) but northern continents cooled (Knorr et al. 2011). Africa and North America also became arid (Begun et al. 2012). Some parts of Eurasia also became arid but others retained moist forests (e.g. deciduous forests) (Ivanov, 2011). The first hominoid fossils, found in East

Africa, date to 23-16 MYA (Fleagle, 2013). One superfamily from the early Miocene is *Proconsuloidea*, an arboreal quadruped neither completely monkey or ape-like (Begun, 2012). *Proconsul* did not have the elongated forelimbs associated with extant apes but had changes in the elbow that correspond with using suspensory locomotion without a tail (Begun, 2015).

In the middle Miocene, temperatures in Africa, Eurasia and North America, dropped even further and the Atlantic ice sheet expanded, lowering the sea level again (Knorr and Lohmann, 2014), and these lower sea levels affected primate dispersals. The Tethys Seaway, which linked the northern Atlantic to the Indian Ocean, was a marine barrier that prevented mammals from migrating between Africa, Europe and Southwest Asia in the early Miocene (Begun et al. 2012). The lower sea levels eliminated the Tethys Seaway, and created land bridges that enabled ape dispersals between Africa, Asia and Europe 17 MYA (Begun et al. 2012). Miocene apes with thick enamel and large jaws adapted to various Eurasian habitats (e.g. deciduous and grasslands) and persisted in Eurasia until the end of the Miocene (Begun, 2015). For example, Asian *Sivapithecus* and European *Dryopithecus* had strong jaws, large molars, and bladelike canines (Ward, 2015). At the end of the Miocene, the trend of cooling and drying intensified to the point that more tropical forests converged into woodland and temperate forests (Begun et al. 2012). Many fauna species such as European Miocene apes could not adapt to the environmental changes, resulting in an extinction event, known as the Mid-Vallesian Crisis (Begun et al. 2012).

1.1.3 PRIMATE DIETARY DIVERSITY

As of September 30, 2014, the International Union for the Conservation of Nature

(IUCN) recognizes 695 primate species and subspecies. Of these, a majority are critically endangered (IUCN Red List, 2015). The Order Primates has a wide geographical range and exploits diverse niches. Central and South America have the highest primate density and contain approximately one third of total primate species and sub-species (211) (IUCN: Primate Diversity by Region, 2014). Africa is similarly rich in primates and is host to 197 species and sub-species (IUCN: Primate Diversity by Region, 2014). There are 183 species and sub-species inhabiting Asia and 105 *lemuriforms* in Madagascar (IUCN: Primate Diversity by Region, 2014). Within these areas, primates exploit a number of ecological terrains from dry-arid savannahs and humid evergreen forests to cold mountainous regions (Kamilar et al., 2013).

The diversity of primate species is characterized by a number of biological and behavioural adaptations, some of which can vary within the same species (Gouevia et al., 2014). There are many areas of primate research that investigate these variations (Clutton-Brock and Janson, 2012). One such area is primate feeding ecology, which addresses the relationship between the environment and primate feeding behaviour (Nakagawa et al., 2009).

Primate diets are difficult to study and complex in composition. They are “variable in content, affected by seasonal habitats, and can change over time” (Hohmann et al., 2006:5). Primate diets include folivory, insectivory, gummivory, grannivory, carnivory, and frugivory (see Table 1.1). Some species are specialized and exclusively consume food within their dietary category; however, several species can switch from being frugivorous to folivorous depending on season, effectively transcending these narrow classifications (Hanya and Chapman, 2013). For example, common brown lemurs

(*Eulemur fulvus*) and geoffroyi spider monkeys (*Atles chamek*) can switch from a fruit-based diet to a leaf-based diet depending on food availability (Johnson, 2007; Chaves et al. 2012). Some primates consume food that their digestive systems cannot accommodate by modifying their behaviour to consume the desired food item. Howler monkeys (*Alouetta spp.)*, for example, are behavioural folivores that reduce their energy expenditure and selectively eat digestible young leaves to account for their lack of specialized gut features for digesting fibrous cellulose of older leaves (Hohmann, 2009). To understand dietary complexities, primatologists focus on a primate's ability (both cognitive and physical) to exploit resources in their environment and in turn, influence their environment through seed-dispersal (Hohmann et al. 2006).

Evaluating seasonal fluctuations in resources can help primatologists understand the relationships between ecosystems and primate diets. Dietary composition can differ amongst habitats (even intra-specifically) based on the types of vegetation found within each habitat (Macho, 2014). Hunt and McGrew (2002) noted that chimpanzees (*Pan troglodytes*) in wetter habitats have a broader diet than those in savannah habitats.

Primates that reside in seasonal habitats (e.g. deciduous forests) face dry seasons where food abundance is low (Brockman and van Schaik, 2005). Some primates respond to seasonality by shifting their diets to low quality resources (such as bark) and remain within their habitat (Chaves et al., 2011). Other primates modify their behaviour by dispersing to find high quality food that is patchily distributed (such as fruit) (Kanamori et al., 2010). During the late 1960s and 1970s, studies including Struhsakher's (1967) on vervet monkeys (*Cercopithecus aethiops)* and Clutton-Brock's (1975) on red colobus (*Colobus badius tephrosceles)*, suggested that there is an inverse correlation between food availability and range area. As resources deplete with changing ecological conditions, primates, specifically larger primates, will increase their home range (Pearce et al., 2012). However, Kelley (2013) pointed out that this pattern is variable and dry-adapted primates in particular will stay close to water and therefore decrease their home range.

Different morphological adaptations also enable primates to remain within a home range during periods of food scarcity. Kay (1984), Masterson (1996) and Wright et al. (2005) highlight how tufted capuchins' (*Cebus apella*) large mastication muscles and general cranio-facial morphology enables them to process hard foods, such as palm fruits, in times of low food abundance. Red uakaris (*Cacajao calvus*) also use specialized broad molars and large canines to consume the husks of unripe fruit (Bowler, 2011) while colobines such as black and white colobus (*Simia polycomos*), have sacculated stomachs (a stomach with four chambers) to digest leaves efficiently (Chapman et al. 2002).

Despite behavioural and morphological adaptations, primates now face extinction due to increased anthropogenic deforestation. It is important to assess critical food sources and understand how primates utilize their habitats for conservation efforts. Each year approximately 13 million hectares of tropical forests are lost due to habitat degradation (Benchimol and Peres, 2014). Primary forests are converted into a mosaic of fragmented forests interspersed with farmland and urban centres (Campbell-Smith et al., 2011). The expansion of agriculture, logging, palm-oil plantations, and human populations are a threat to primate persistence worldwide (Vasudev et al., 2015).

As fruiting trees are removed, the natural landscapes utilized by primates no longer contain sufficient primate food sources. Furthermore, the fragmentation of forests threatens primates with poor dispersal abilities (Menard et al., 2014). In response to environmental changes, primates that exhibit dietary plasticity alter their diet to correspond to a restructured environment (Baranga et al.2012). Studies that evaluate the changes in primate diets due to the destruction of habitat primarily focus on herbaceous vegetation, fruit consumption, and cultivated crops. For example, Campbell-Smith et al. (2011) looked at the increased consumption of jackfruit and rubber tree bark by Sumatran orang-utans (*Pongo abelli)* in an agroforest system. Menard et al. (2014) evaluated Barbary macaques (*Macaca sylvanus*) subsistence on acorns and herbaceous leaves in a human-modified cedar-oak forest.

The navigation of anthropogenic landscapes by primates also encourages crop raiding. Primates consume cultivated plants to compensate for the loss of the plants they originally ate in their forested habitat (Canale et al. 2013). Farmers often view the primates as pests and shoot them to prevent the destruction of their crops (Riley, 2013; Guiness and Taylor, 2014), for example, Kibaja (2014) noted that farmers shot Ashy red colobus (*Piliocolobus tephrosceles*) that ate their bean seeds in Mbuzi, Africa. Hunting related to crop raiding affects endangered primates because their populations are already low. For instance, Sumatran and Bornean orang-utan populations have each declined to around 6600-7000 animals (Abram, 2015). Campbell-Smith et al. (2012) found that 10% of farmers in Batang Serangan, Sumatra shot orang-utans as a response to crop damage and Meijaard et al. (2011) reported that humans killed 1,750 Bornean orang-utans in 2010. In light of the already endangered status of Sumatran orang-utans, even a few deaths can dramatically impact population recovery. The population suffers reduced genetic variability, impacts their ability as a species to adapt to changing environments, and individuals become isolated, decreasing mating opportunities (Abram, 2015). Additionally, due to primates' slow life histories, even when reproduction is successful, population growth takes a long time (Meijaard et al.2011).

One area of primate diets that has seen very little research is that of the ecological patterns of large invertebrate and vertebrate consumption by primates. Moreover, there is little research which questions if the consumption of large invertebrates and vertebrates (hereafter referred to collectively as "meat") has changed due to the conversion of natural forests into anthropogenic landscapes. Large invertebrates include animals such as mollusks, crabs and millipedes, while vertebrates encompass small to medium sized mammals, reptiles, amphibians and birds (Watts, 2012; McGrew, 2014).

Folivorous primates rarely consume meat, while insectivores, frugivores and omnivores are known to consume varying amounts of meat. However, the only 100% carnivorous primate is the nocturnal tarsier (Raubenheimer and Rothman, 2014). Tarsiers prefer the tropical understory where there is an abundance of arthropods, lizards, snakes, and frogs (Gursky, 2002; Merker and Yustian, 2008). Tarsier morphology is unique amongst primates, which allows this specialized diet. Tarsiers are small-bodied like other nocturnal primates (see section 1.1.1), but they also have very generalized stomachs (with a short caecum), use vertical clinging and leaping locomotion, and exhibit eye morphology adapted for nocturnal vision and hunting (Crompton 2010; Rosenberger and Prueshoft, 2012). Vertical clinging and leaping enables tarsiers to quickly pounce on their prey and increases capture efficiency (Crompton, 2010). Tarsiers' uniquely developed fovea, which consists of an all-rod retina, also intensifies visual acuity for capturing prey (Jablonski, 2003). For instance, it permits tarsiers to capture stationary prey whereas other nocturnal primates rely on movement to locate prey (Siemers et al., 2012). The adaptation of the fovea “provides tarsiers with the most acute vision of all primates” (Jablonski, 2003:44). Tarsiers also exhibit jaw morphology that ~~has~~ developed differently from many primates (Jablonski, 2003). The large jaw adductors (*M.temporalis*) facilitate wide jaw opening and forceful closure, which allows tarsiers to consume their prey whole (Jablonski and Crompton, 1994).

Both omnivore and frugivore diets consist of fruit, plants, and animal food (Hohmann et al., 2006). The proportions of these foods however can vary between and within species. One reason the contribution of meat to omnivore and frugivore diets has rarely been explored is that there is generally very little meat in their diets. For instance, the diet of collared lemurs (*Eulemur collaris*) that inhabit littoral forest fragments is comprised of 0.8% meat (Donati et al., 2011) and the diet of vervet monkeys (*Chlorocebus aethiops*) consists of just 2.7% meat (Pruetz and Isbell, 2000). Even the diets of chimpanzees, one of the omni-frugivores that consume the highest amount of meat, are comprised of, at most, 7.5% meat (Fahy et al.2013).

Early research on omnivore and frugivore meat consumption was limited to chimpanzees, baboons *(Papio spp.)* and capuchins (*Cebus spp.).* Jane Goodall made an early observation in 1963 of Gombe chimpanzees capturing red colobus (Mitani and Watts, 2001). Hausfater (1976) later conducted a detailed study on forty-seven predation episodes by olive baboons (*Papio anubis).* During the 1970s, only captive capuchins were observed eating meat; however, narratives by locals living near capuchin habitats made primatologists aware that wild capuchins also ate meat (Izawa, 1978). Thus, Izawa (1978) conducted a survey in La Macarena National Park, Colombia, of frog consumption by black-capped capuchins, and Butynski (1982) conducted a comparative survey of predation patterns by primates. Since the year 2000, reports on predation by capuchins and other primate species has increased considerably (Stewart et al., 2008).

Primatologists have proposed a number of hypotheses to explain predation by primates. Early hypotheses inferred that there was a nutritional basis for primate meat consumption. For instance Hausfater (1976) suggested that primates eat meat to obtain micronutrients like vitamin B12, while Gaulin and Kurland (1976) hypothesized that primates consume meat to obtain energy and calories, as it is calorie dense food. One explanation proposed by Teleki in 1973 and Strum in 1981 was that primates engage in predation when there are abundant prey species available and a low density of larger competing carnivore species (Fedigan, 1990). Yet, Fedigan (1990) later noted that predation still occurs at sites like Santa Rosa, Costa Rica, where carnivores are relatively abundant. Leca et al. (2007), Stewart et al. (2008), and Strum (2012) proposed that predation is culturally transmitted and a sign of increased cognitive abilities, although Leca (2007) concluded that predation occurs too rarely to be transmitted across multiple generations. Ultimately, there is no hypothesis that can explain predation for all primates because predation varies across all primate groups.

1.2 BACKGROUND ON OMNI-FRUGIVORE DIET AND BIOLOGY

1.2.1. CLASSIFICATION OF PRIMATE DIETS

I used the dietary categories depicted in Table 1.1 to conduct my research. These categories were taken from the literature on dietary ecology. Since I will discuss omnivores and frugivores, I will henceforth refer to both dietary categories together as ‘omni-frugivores’ for brevity.

Table 1.1 Primate Dietary Classifications

Diet Type	**Definition**	**Source**
Frugivory	~67%of the diet is fruit while the rest is bark, young leaves, seeds, flowers, nectar, pollen, insects, invertebrates and vertebrates	Milton et al., 2005; Schrier et al., 2009
Folivory	A diet that primarily consists of young and mature leaves, as well as fruit, flowers, plants, nectar, lichens, seeds, bark and insects.	Chapman, 2013; Sayers, 2013
Frugivory-folivory	A diet that is frugivorous but switches to folivorous during periods of low fruit abundance	Schrier et al. 2009
Granivory	Seeds are the main staple in the diet. Fruit and flowers are also consumed. Leaves are not relied upon.	Benchimol and Peres, 2014
Gummivory	Most of the diet is made up of the saps and gums of trees. Fruit, exudates, insects and vertebrates are also eaten with frequency.	Thompson et al.,2013
Insectivory	Insects are the main component of their diet, supplemented with fruit and gums.	Gursky, 2002
Omnivory	A diet that contains ~50% fruit, bark, young leaves, seeds, flowers, buds, cacti, nectar, pollen, insects, invertebrates and vertebrates.	Kamilar et al., 2013

1.2.2 GENERAL DESCRIPTION OF OMNI-FRUGIVORE DIETS

Omni-frugivores exhibit a preference towards fruit but also consume other plant parts, underground storage organs (USO), nuts, and fauna (insects, invertebrates and vertebrates) (Hohmann, 2009). Their dietary and behavioural flexibility enables them to exploit domesticated crops, discarded tourist food (e.g. chicken, french fries) and garbage (Fuentes et al., 2011; Riley, 2013). For instance, long-tailed macaques (*Macaca fascicularis)* exploit the rice and chicken placed as offerings at a temple in Pendangtegal, Warna Wana, Bali (Fuentes et al. 2011). Although omni-frugivores diets are flexible, meat does not make up a substantial portion of omni-frugivore diets nor is it a commonly sought-after food item (Hohmann, 2009). Kay (1984) argued that the rapid basal metabolic rate of primates weighing less than 500g makes insects beneficial for smaller-bodied primates. Primates that weigh more than 500g struggle to gain the nutritional benefits of insects due to their slow basal metabolic rates and size (Kay, 1984). Smaller primates have a greater surface area/volume ratio compared to larger ones and thus lose heat more quickly (Lambert, 2002). Therefore, smaller primates use more metabolic energy to maintain their core body temperatures, leading to a high basal metabolic rate (Snodgrass, 2009). Smaller primates also have smaller gut volumes than larger primates (Claus et al.2008). As larger primates increase in size, so does their gut volume and digestion time (Clauss et al. 2008). The longer digestion time allows them to efficiently extract nutrients from lower quality food (e.g. leaves) (Lambert, 2002). Small primates with shorter digestion times have to consume higher quality, more digestible food in order to absorb nutrients more quickly to produce heat and energy (Lambert, 2002).

Insects comprise the largest percentage of meat in omni-frugivore diets, even though invertebrates and vertebrates provide more protein for omni-frugivores over 500g (Kay, 1984; McGrew, 2014; Raubenheimer and Rothman, 2014). Large invertebrates and vertebrates are harder to exploit than insects because they are more patchily distributed, need more energy to capture, and require specialist knowledge and techniques to exploit the resource (e.g. hammer and anvils to break open hard shells of crabs) (Mannu and Ottoni, 2009; Raichlen et al., 2011; McGrew, 2014). I will focus on large invertebrates and vertebrates as they provide more protein; yet paradoxically comprise a smaller portion of omni-frugivore diets.

1.2.3 OMNI-FRUGIVORE DIGESTION

An omni-frugivore's degree of adaptability is partly enabled by their physiology. The ability of primates to absorb nutrients from plant sources is dependent upon how efficiently they can digest these difficult to digest foods (Milton, 1999; Lambert, 2002; Sawada et al., 2010). The nutrients in the food become increasingly potent the longer that the food remains in the digestive tract (Caton et al., 1996; Milton, 1999; Sawada et al., 2010) Omni-frugivores such as black-capped capuchins (*Sapajus apella*) and lion-tailed macaques (*Macaca silenus*) exhibit fast metabolisms and a simple stomach with a single chamber (a hindgut) (Lambert, 2002; Clauss et al., 2008; Snodgrass et al., 2009) and thus prefer resources that are easily digestible.

Fruit is high in caloric content and sugar whereas mature leaves contain higher levels of cellulose and secondary compounds (Wasserman and Chapman, 2003; Sawada et al., 2010; Hanya and Chapman, 2013). Mature leaves are therefore more difficult to break down for all hindgut fermenters than fruit (Lambert, 2002). Secondary compounds (e.g. alkaloids and tannins) act as the plant's defense mechanism against predators and are toxic to many mammals (Wasserman, 2011; Sirianni et al., 2013). Alkaloids can inhibit enzyme production and interfere with neurotransmission (Wasserman, 2011), while tannins render protein in leaves inaccessible to animals (Chapman and Lambert et al., 2013).

Omni-frugivores also have large colons and caecums for extended microbial fermentation of resources (Lambert, 2002; Clauss, 2008; Sawada, 2010; Lambert, 2011). Milton (1999) noted that apes have a larger gut volume in the colon (~45%) than humans.

The large gut enables omni-frugivores to absorb more nutrients from plant resources than humans (Snodgrass et al., 2009). Consequently, although humans can consume fruit and legumes, they must supplement their diet with more meat and carbohydrates (Clauss et al., 2008; Snodgrass et al., 2009).

1.2.4 FOOD SELECTIVITY

Initially, primatologists suggested that primates select resources that provide the most amount of energy for the least amount of foraging time (Garber, 1984). As such, the conclusion was that food with high energetic content equated with a high quality diet. Conversely, more recent studies (Chaves et al., 2011; Emery-Thompson, 2013; Heesen et al., 2013) suggest that high energy and caloric content alone do not equate with a high quality diet. Primate resource selectivity is influenced by 1) protein-to-fibre ratios, 2) macro and micronutrients, and 3) avoidance of secondary compounds in conjunction with energetic content of a resource (Felton, 2009; Zhao et al., 2013). I discuss protein to fibre ratios in more detail below.

Primates select food items that have a higher proportion of protein compared with fibre (Wasserman and Chapman, 2003). Protein controls metabolic reactions, comprises hormones and structural molecules, and replicates DNA (Hinde and Millegan, 2011) and primate diets must contain at least 7-11% of protein to sustain their bodily functions (Chapman and Wasserman, 2003; McGrew, 2014). Nitrogen is an element of amino acids that primatologists use to analyze protein content in food sources (Felton et al., 2009; Zhao et al., 2013). There must be at least 1.1-1.8 % nitrogen in fruit and leaves for a primate to adequately absorb enough sustainable protein (Ganzhorn et al., 2009).

High fibre in an individual’s diet effectively limits protein absorption (Rode et al., 2006;

Hanya et al., 2011; Kayode et al., 2012). Omni-frugivores often select young leaves and fruit because these contain more protein and less fibre compared with mature leaves (Chapman et al., 2002). As such, omni-frugivores do not need to consume a substantial amount of meat to obtain sufficient protein, since there are usually easily accessible protein-rich plant sources available (Hohmann, 2009). However, Hofrieter et al., (2010) and Oelze et al., (2011) suggested that there is an inverse correlation between meat ingested by bonobos (*Pan paniscus)* and protein availability in plants: bonobos consume more meat in habitats where the protein levels of plant sources are low. Few studies that focus on meat eating amongst primates also include the protein contributions from plant resources, and therefore conclusions are still tentative.

1.2.5 OMNI-FRUGIVORE BIOENERGETICS AND ACTIVITY BUDGETS

The energy conservation hypothesis suggests that primates are constrained by how much nutrition and energy an individual can gain from the environment (Wright, 1999; Snodgrass et al., 2009; Raichlen et al., 2011). Energy conservation affects the activity budgets of primates. Activity budgets are defined as "the way that a given primate species strategically allots time to key activities (such as feeding, resting and traveling)" (Vasey, 2005: 24), and are directly related to primate metabolism and to energetic needs that change across seasons or reproductive stage (Vasey, 2005).

Hunting involves a considerable portion of omni-frugivore daily activity budgets when they engage in it (Hladik et al., 1999; Clauss et al., 2008). Large invertebrates and small-medium vertebrates can move quickly, and can also attack the primate as an anti-predator strategy (McGrew, 2014). These prey characteristics make the prey more energetically costly to exploit compared to fruit. For example, Hohmann and Fruth (2008) noted that at

Lui Kotamba in the Democratic Republic of Congo, bonobos (*Pan pansicus*) spend over two hours to catch duikers (a medium sized antelope). There is also the risk that the prey will not actually be captured and the energy spent by the predator to hunt will be wasted (Young et al., 2012; McGrew, 2014).

Forest type can affect the probability of catching prey (Hohmann, 2009). Rose (1997) suggested that it is easier to catch prey in drier forests as well as secondary forests. She noted that the secondary forests in Santa Rosa, Costa Rica contain patchily distributed trees that are all in different stages of regeneration. The semi-cleared forests and reduction in canopy density increases the visibility of the prey (Rose, 1997). Wet tropical rainforests, such as the Tai Forest in Côte d'Ivoire have denser tree canopies compared to drier forests (Boesch, 1994). As a result, omni-frugivores in drier forests expend less energy catching prey and increase the likelihood of success (Rose, 1997; Hohmann, 2009).

To offset the cost of reduced visibility in a wet forest, some primates adjust their hunting strategies through cooperative hunting and by increasing the size of hunting parties (Gilby and Wrangham, 2007; Young et al., 2012). Cooperative hunting occurs "when a hunter hunts with a companion" (Boesch et al. 1994: 653), and serves to pool a troop's energy together to minimize individual energy expenditure and the time spent hunting (Strum, 2012). Pooled energy is defined as "subsidized energy in the form direct calorie subsidies or division of labour" (Kramer et al., 2010:139). By reducing the time spent on hunting through increasing the number of participants, omni-frugivores can conserve their energy (Raichlen et al., 2011). The Tai Forest chimpanzees in Côte d'Ivoire, form hunting parties of approximately ten males, whereas chimpanzees that inhabit open woodland and gallery forests in Gombe and Mahale Africa form smaller hunting parties (on average eight chimpanzees) (Uehara et al., 1997).

The size of both primate and prey also affects a primate's energy expenditure and hunting strategy. Small omni-frugivores that weigh less than 500g, such as tamarins (*Saguinus spp.*) and marmosets (*Callithrix spp.*) can hunt smaller prey (e.g. lizards, snakes, and squirrels) independently for a low energetic cost and high caloric return because they are quick and their prey are comparatively large to their bodies (Cunha et al. 2006; Nadjafzadeh et al. 2008). Larger Omni-frugivores, such as chimpanzees and baboons, have slower basal metabolic rates and physical speeds, tend to consume large (around 0.45kg) prey in order to receive enough protein but require cooperation with other hunters to offset the cost of exploiting these large species (Uehara et al., 1997). For instance, male yellow baboons (*Papio cynocephalus*) that generally weigh ~24 kg, use cooperative hunting to capture gazelles, which are heavy and can outrun a single baboon (Hohmann, 2009).

1.3 RELATIONSHIP BETWEEN ECOLOGY AND OMNI-FRUGIVORE DIET

1.3.1 ECOLOGICAL VARIATION AND DIET

Primates evolved as seed dispersers (Jordano et al., 2011; Tsuji et al., 2011) and are adapted to eat fruit and leaves rather than meat, which may explain why they have a low percentage of meat typically in their diet (Chapman et al., 2013; Hanya and Chapman, 2013; Rosenberger et al., 2013). Sussman (1991) posited that the role of seed dispersal by primates arose because Euprimates co-evolved with angiosperms around 80 million years ago. The warming trend and shift to tropical conditions culminated in an adaptive radiation of new flowering plants and primates at the end of the Paleocene (Sussman et al. 2013). Ancestral primates filled the niche, aiding in the germination of angiosperms (Sussman et al., 2013).

Primates assist in maintaining their habitat through niche construction as seed dispersers (Fuentes, 2012). As defined by Fuentes, “niche construction is the altering or building of a niche via the mutual interaction between an organism and their environment” (Fuentes, 2012:110). Omni-frugivores account for approximately 60-80% of regeneration cycles in plants (Jordano et al., 2010; Hawes and Peres, 2013; Albert et al., 2014). Primates support plant regeneration by spreading seeds through their faeces (Chapman et al., 1995; Zárate et al., 2014; Gonzalez-Zamora et al., 2014). They also propagate plants by spitting out un-masticated seeds or discarding indigestible seeds (Chapman et al. 1995; Lambert and Garber, 1998; Stevenson, 2000; Beaune et al., 2013;Razafindratsima et al. 2014).

Omni-frugivore diets can vary according to the niche they help construct. In savannah and woodland habitats tree diversity per hectare can be as low as one or two species compared to wet tropical evergreen forests, which can contain over 200 species per hectare (Singh and Sharma, 2009; Domínguez-Rodrigo, 2014; Macho, 2014). Woodland dwelling primates such as olive baboons (*Papio anubis*) (Kunz and Linsenmair, 2007) and vervets (*Chlorocebus aeithops*) (Pruetz and Isbell, 2000) consume more grasses and USOs compared to those in tropical habitats and thereby spread more grass seeds than tree seeds (Sing and Sharma, 2009). Conversely tropical primates consume more fruit and leaves and thus disperse more seeds of fruiting tree species.

The nutritional content of resources across continents and within habitats can also contribute to variation in diets. For instance, the protein synthesis of native plant life across continents is affected by a multitude of factors including temperature, moisture and soil composition (Ganzhorn et al., 1992; Gonzalez-Zamora et al., 2011). Soil salinity can inhibit protein absorption within plant resources as it reduces leaf surface area, preventing photosynthesis (Vranova et al., 2011). Primates across continents and habitats therefore have access to a variety of resources that contain variable amounts of protein. A notable example is that fruit growing in Central and South America contains more protein compared to fruit in Madagascar (Ganzhorn et al., 2009).

Wet tropical evergreen forests also contain plant resources that differ in protein concentrations based on the elevation of the canopy and the plant's position in the forest (often referred to as the canopy effect) (Ganzhorn et al., 1992; Chapman and Rothman et al., 2012). Plants are able to create their own nutrients through photosynthesis, where the chlorophyll in leaves absorb solar energy and use it to convert water and carbon dioxide into sugar (Hill, 1970; Ganzhorn et al.1992). When a plant absorbs too much sun it transforms extra sugars into starch and then breaks the starch molecules down into other compounds like protein and fat (Ganzhorn et al.1992). The canopy effect suggests that the leaves located in the upper and mid-portion of the canopy have access to more sunlight, and thus consist of more protein compared to plants in the understory (Ganzhorn, 1995; Chapman and Rothman, 2012). Thus, arboreal primates in the upper portion of the canopy gain access to resources containing more protein. In Salonga National Park, D.R.C, dryas guenons (*Cercopithecus dryas)* located in higher portions of the canopy have elevated levels of protein in their diet compared to sympatric bonobos, who consume food primarily on the ground (Oelze et al., 2011).

1.3.2 RESPONSES TO RESOURCE SCARCITY

Seasonality is linked to ambient temperature and rainfall within a habitat. There is a positive correlation between rainfall and food availability (Gonzalez-Zamora et al., 2011), therefore primate food availability fluctuates during wet and dry seasons in most habitats (Hanya et al., 2013). The increased moisture during wet seasons enables plants to receive the nutrients they require to grow (Chaves et al., 2012). In tropical rainforests such as those in Guyana for instance, rainfall nearly doubles during wet seasons (Pereira et al., 2014). As such, a majority of omni-frugivores reside in lush forests during wet seasons, with access to an abundance of resources (Wallace et al., 2005; Swedell et al., 2008).

The nutritional composition of resources can change across seasons. Forests contain fewer protein-rich plant sources during dry seasons than wet seasons (Lambert, 2009; Gould et al., 2011; Hanya et al., 2011). Chapman and Rothman et al. (2012) noted that, in seasonal dry forests, the protein content in fruit and leaves is commonly 43% lower in dry seasons than wet seasons. For example, in Tsinjoarivo, Madagascar, the protein content of young leaves consumed by Diademed sifakas (*Propithecus diadema*) dropped from 14.5% (+/- 6.4) in the abundant season to 12.4% (+/- 6.9) in the lean season (Irwin et al. 2013) and in Gashaka, Nigeria, chimpanzees can access fruit with less than 5% protein during dry seasons compared to 9% in wet seasons (Hohmann et al. 2010).

The study of fallback foods and keystone resources are common approaches to understanding primate responses to food shortages (Chapman and Lambert et al., 2013). For the purposes of my thesis, **fallback foods** are defined as: food exploited during periods of low food abundance (Marshall and Wrangham, 2007). K**eystone resources** are defined as: resources that are important to the persistence of many species in a community, even though the resource may be rare or scarcely available (Constantino and

Wright, 2009). Primates feed on mature leaves, piths, and other herbaceous vegetation when food is scarce (Marshall and Harrison, 2011). Recently, Marshall and Harrison (2011) noted that the dietary quality of fallback foods might not be consistent across primate taxa due to variation in morphology, behaviour, and plant species available within a habitat. As such, there are no fallback foods that are attributed to all primates (Chapman and Lambert et al, 2013). Moreover, omni-frugivores are unable to subsist long term on a single fallback food (Hanya and Chapman, 2013). Although primates can acquire specific nutrients from a resource, no food item provides an adequate diet with all the right proportions of nutrients (Altmann, 2009). Instead, primates consume multiple food items that are still available during food shortages (Chapman and Lambert et al., 2013).

Meat for instance is a high quality food item that is consumed by omni-frugivores at a greater frequency during periods of food scarcity and some researchers thus hypothesize it to be a fallback food (Hohmann, 2009). A majority of primates consume prey during dry seasons to account for the lack of nutrients present in plants (Surbeck and Hohmann, 2008; Hohmann, 2009; Hofrieter et al., 2010). For example, during dry seasons white-faced capuchins (*Cebus capuchinus*) consume infant white-nosed coatis (Fedigan, 1990; Rose, 1997; Palmiera and Pianca, 2012), bonobos eat duikers (Hohmann and Fruth, 2008; Surbeck et al.2008), and western black-crested gibbons (*Nomascus nasutus*) consume lizards in the winter (Fan et al. 2011). In contrast however, some omni-frugivores vary intra-specifically in their seasonal preference for meat and as such is not a fallback food for these species. Chimpanzees in the Tai forest consume red colobus during wet seasons, while chimpanzee populations at Ngogo, Uganda consume red colobus in dry seasons

(Boesh, 2002; Gilby et al., 2008). Some omni-frugivores consume prey regardless of the season. Common brown lemurs that reside in a gallery forest of southern Madagascar have been observed consuming meat resources such as chameleons and infant ring-tailed lemurs throughout all seasons (Jolly et al. 2000; Simmen et al. 2003).

In the 21st century deforestation has removed critical keystone resources (e.g. *Ficus* spp.,) as forests are cleared for human use (Oates, 2013). It is estimated that between 1990 and 2012 over 149 million hectares of forest were lost due to deforestation worldwide (Estrada, 2013). According to The IUCN (2014), 56% of primate species are critically endangered. In fact, 94% of Madagascar's lemur species are vulnerable to extinction (Magiera and Labanne, 2014; Schwitzer et al., 2014). Habitat loss has caused intra and inter-specific competition in primate communities due to increased encounters with conspecifics and other primates at confined borders and forest fragments (Oates, 2013). As global deforestation has removed keystone resources, reports of meat consumption have increased in primate literature. Most of these observations have occurred in fragmented forests where there are fewer resources (Carretero-Pinzon et al., 2008; Stewart et al., 2008; Hardus et al., 2012).

1.4 PREDICTIONS

1.4.1 NICHE AND HABITAT VARIATION IN MEAT CONSUMPTION

Niche separation is "the spatial and dietary separation of sympatric species in a single habitat through the occupation of different strata in the forest canopy" (Zhao et al., 2014: 125). Niche separation evolved as a mechanism to reduce resource competition (Zhao et al., 2014). Resources that are located at a higher elevation within the canopy are more diverse than resources on the ground (Oelze et al., 2011); therefore, arboreal omni-frugivores can access a greater diversity of plant species in the canopy due to their morphological adaptations for moving on thin branches (McGraw and Daegling, 2012). Terrestrial omni-frugivores also have longer daily path lengths than arboreal primates, which could increase their chances of encountering prey (Hemingway and Bynum, 2005).

Omni-frugivores that live in tropical or deciduous forests consume more flowers and fruit species compared to those in drier habitats (Brockman and van Schaik, 2005). Some omni-frugivore species can also occupy multiple habitats and exhibit different diets based on the resources available (Hill and Dunbar, 2002). Olive baboons in Kibale National Park, Uganda inhabit moist semi-deciduous forests (Johnson et al. 2012), which contrasts with olive baboons in Laikipia, Kenya which are found in woodland habitat (Barton and Whitten, 1994). The olive baboons in Kibale select food low in hemi-cellulose, and they do not select food for protein to the same extent as those in Kenyan woodland habitats (Johnson et al., 2012). There are few potential prey items that live in savannah habitats, as drier habitats are a harsh environment in which to survive (Domínguez-Rodrigo, 2014; Macho, 2014). Nevertheless, since savannah habitats contain few tree species, there is improved visibility for omni-frugivores to observe prey (Rose, 1997; Domínguez-Rodrigo, 2014). The shrubs and sedges within woodland and grassland habitats are also shorter in height compared to trees in the wetter forests, for example *Acacia spp.* are just 1.5-3.0 metres in height (Pruetz et al., 2000) while palm trees in a Peruvian tropical forest are 28 metres in height (Palmenteri et al. 2012). This shorter tree height in dry forests increases primate visibility, useful for hunting (Pruetz et al., 2000).

Dry forests can be exposed to lengthy dry seasons, which reduce fruit biomass and changes forest structure (Hanya et al., 2013). For example, western and southern

Madagascar dry forests are susceptible to hot lengthy dry seasons that cause droughts and scarcity of high quality plant sources for the primates living within them (Gould et al. 1999; Gould et al., 2003; Ratsimbazafy, 2007; Sato, 2013). A majority of omni-frugivores seem to consume more meat during dry seasons (Hohmann, 2009; Raubenheimer and Rothman, 2014; McGrew, 2014), and a lack of plant protein might be a contributing factor to this trend (Oezle et al., 2011). Currently, there is limited research on niche separation and habitat choice in relation to meat consumption by omni-frugivores. One question that has yet to be investigated is: do omni-frugivores consume varying amounts of meat based on their strata occupation, habitat choice or season? Based on the theories and examples above, I make the following testable predictions:

PREDICTION 1: *I predict that arboreal omni-frugivores include a significantly lower percentage of meat in their diets compared to terrestrial omni-frugivores. Since the resources within the canopy are diverse, arboreal primates can already access an abundance of plants with adequate levels of protein (Rose, 1997). Therefore, arboreal omni-frugivores do not require meat as a nutritional supplement to the same extent as those on the ground. I further predict that there is a positive correlation between daily path lengths of terrestrial omni-frugivores and the percentage of meat in their diets. The longer daily path lengths of terrestrial omni-frugivores (Hemingway and Bynum, 2005) may offer more opportunities for prey encounters.*

PREDICTION 2: *I predict that omni-frugivores residing in drier habitats exhibit a significantly higher percentage of meat in their diets compared to those inhabiting wet-evergreen and deciduous forests. The enhanced visibility and few plant resources within drier habitats increase the chances of catching prey, which in turn influences the higher percentage of meat within most terrestrial omni-frugivore diets (Fedigan, 1990; Rose, 1997).*

PREDICTION 3: *I predict that there is a positive correlation between the percentage of meat in the diets of omni-frugivores and dry seasons associated with seasonal habitats. The reduction in fruit biomass that occurs during dry seasons increases a primate's susceptibility to nutritional deficiency (Ganzhorn et al., 2009). As such, omni-frugivores will increase the percentage of meat in their diets during dry seasons. There will also be a greater proportion of dry season hunters to accommodate resource scarcity.*

1.4.2 RELATIONSHIP BETWEEN PROTEIN AND MEAT CONSUMPTION

Primate food preference is influenced by the protein availability in the resources that are available in their habitat (Ganzhorn et al., 2009; Hanya et al., 2011). For example, in Madagascar, there are more folivorous primates than in South America and Asia, because the protein content is higher in Malagasy leaves compared to fruit (Ganzhorn et al., 2009). In contrast, South American and Asian forests contain more frugivorous primates, as the protein content is higher in neo-tropical fruit compared to leaves (Ganzhorn et al., 2009). The continent that a frugivore inhabits thus affects its access to protein-rich plant resources. Frugivores with less access to protein-rich plant sources might consume more meat as a dietary supplement. Since primate food preference is influenced by the protein availability in plants (suggested by Ganzhorn et al., 2009), one question that still requires more research is: does the protein content in plants affect the amount of meat consumed by primates? Below is the testable prediction that I will use to examine this question.

PREDICTION 4: *I predict that there is an inverse correlation between high protein content in plant resources and the percentage of meat in omni-frugivore diets. Thus, omni-frugivores inhabiting Africa, Madagascar and Asia will have a significantly higher percentage of meat in their diets compared to neo-tropical omni-frugivores because such forests contain fewer protein-rich plant sources.*

1.4.3 DIVERSITY OF HUNTING STRATEGIES

Omni-frugivores that opportunistically hunt for meat rely on their own energy to catch their prey, thus it is physiologically costly if there is no return (Hohmann, 2009). Moreover, hunting individually leaves less time to rest and socialize (Sato, 2013). Primates that hunt cooperatively (e.g. baboons) are able to pool their energy and hunt more often (Hohmann, 2009; Strum, 2012; Emery-Thompson, 2013). Furthermore, omni-frugivores that hunt cooperatively sometimes share meat with other troop members (Leca et al., 2007). In omni-frugivore species, there are sex differences when hunting for meat (Rose, 1997). Because lactation is energetically costly for females, they tend to conserve energy by reducing transit and foraging times, and thus forgo meat for other accessible plant foods (Brockman and van Schaik, 2005; Hohmann, 2009; Murray et al., 2009). However, meat sharing in chimpanzees, for example, offers some females opportunities for meat intake by acquiring meat from males (Hohmann, 2009; Surbeck et al., 2009). In some primate species the non-gestating females hunt, e.g. non-gestating female bonobos are known to be the primary hunters compared to males (Hohmann and Fruth, 2008), and there are female hunters in many baboon species (e.g. olive, yellow and chacma baboons) (Strum, 1975; Akosim et al., 2012). Much research has been conducted on the behaviours involved with cooperative hunting, opportunistic hunting and meat sharing (e.g. Boesch et al.1994; Rose, 1997; Mitani and Watts, 2001; Gilby et al. 2007; Strum, 2013), however no researchers have asked the following questions: what is the difference in the amount of meat consumed between opportunistic and cooperative hunters? Do meat-sharing species ingest more meat? Based on the theories above, I will examine this question and make a prediction below.

PREDICTION 5: *I predict that there is a significantly higher percentage of meat in the diets of cooperative hunters. Meat sharers also consume a significantly higher percentage of meat. Cooperative hunting decreases the energy expenditure of one individual through pooled energy, which therefore increases the opportunities for successfully capturing prey and meat sharing (Hohmann, 2009; Strum, 2012; Emery-Thompson, 2013).*

1.4.4 MEAT CONSUMPTION AND DEFORESTATION

Fragmented forests decrease the home ranges of primate species, while simultaneously increasing the potential for intergroup encounters, feeding competition between primate groups, and prey-predator interactions (Amsler and Watts, 2013; Chapman et al., 2013; Gilby, 2013). As critical keystone resources and tree species are removed, omni-frugivores are left with fewer protein sources. Vertebrate prey is a food source that is available to omni-frugivores residing in these anthropogenically-modified habitats.

Butynski (1982) noted that during the 1970s there were fewer than 450 observed instances of vertebrate predation, with 220 attributed to baboons and 143 associated with chimpanzees. However, in the 21st century, primates previously considered to be non-meat eaters, such as black-crested gibbons, have now been observed consuming prey (see Fan et al. 2009; Fan and Jiang, 2009; Hardus et al. 2012). Moreover, omni-frugivores that are identified as meat-eaters have now being observed eating different prey items than in the past (Stewart et al., 2008). Most of these sightings have occurred in habitats with few resources. For example, Young et al. (2012) observed that Barbary macaques in Atlas Mountains of Morocco had never been observed eating meat but now hunt and consume rabbits, birds, and eggs. Such meat consumption was reported after human expansion in the early 2000s forced Barbary macaques higher into the mountains (Young et al., 2012).

Stewart et al. (2008) suggested, however, that the increased observations of meat consumption are in fact due to primatologists paying more attention to their animal subjects. I must keep methodological bias in mind when conducting my research. New methods in focal animal sampling such as web-cams have enabled primatologists to watch their subjects for increased periods of time (e.g. Tan et al., 2013; LaFleur et al., 2014; Pebsworth et al., 2014). Leca et al. (2007) used web-cams to observe a population of Japanese macaques (*Macaca fuscata)* scavenge fish on Koshima Island, a rare event. In relation to the theories and examples discussed above, a question yet to be explored is: has the percentage of meat in primate diets increased over the past 45 years? If so, is increased meat consumption related to deforestation or is it a sampling artifact connected to newer technology and methods used by primatologists? Below is my prediction with regards to this question.

PREDICTION6: *I predict that the percentages of meat in omni-frugivore diets have risen significantly in the past 45 years, particularly in areas of human expansion and disturbance. Such an increase may have occurred because keystone plant food resources, a former source of protein, have decreased due to habitat disturbance.*

CHAPTER 2: RESEARCH METHODOLOGY

2.1 STUDY SUBJECTS

My study subjects are diurnal omnivorous-frugivorous primates. As there are many omni-frugivore primates, I created a list of omni-frugivore species based on the characteristics described in chapter one. I also referred to the descriptions of primate diets available on the PrimateInfo Database (see http://pin.primate.wisc.edu/factsheets/).

I incorporated omni-frugivores that do not eat meat as they have the capacity to ingest it. Non-meat-eating omni-frugivores are important to consider in the context of ecological pressures. I did not include nocturnal insectivores because they consume a high proportion of fauna. Nocturnal insectivores also exploit different resources compared with diurnal omni-frugivores. Including nocturnal insectivores in my analysis could have affected my results, as there would have been too many outliers since I focus on primates that consume small quantities of meat. I excluded folivores for the opposite reason; folivores consume such small amounts of meat that there was not enough data available to conduct my research. I also omitted insects as meat sources because omni-frugivores consume a higher proportion of insects compared to large invertebrates and vertebrates (Hohmann, 2009).

I recorded at least two omni-frugivore species for each continent and habitat to reflect their broad distribution patterns. Overall, my sample consists of 51 primate populations. Some of these 51 are the same species but from different sites, to reflect intra-specific variation in habitat choice. I included 15 primate populations from Africa; 16 from Asia (one from Japan, seven from Indonesia, four from China, two from Thailand and two from India); 14 from the Neotropics (12 from South America and two from Central America); and six primate populations from Madagascar (refer to Appendix

I). These study primates reside in a variety of habitats that range from savannah-woodland environments to swamp and coniferous forests.

Many primate species in my study navigate anthropogenically-altered landscapes and are increasingly threatened by human encroachment (Appendix 7 contains the conservation status of my sampled species). The 12 species (in my study) that reside in South America are forced to reside in fragmented forests. One such species, the tufted capuchin, occupies 98% of 129 south Amazonian fragmented forests (Benchimol and Peres, 2013). The degree of isolation caused by the nature of the surrounding matrix, hunting pressures within patches, and amount of forest disturbance compromise their home range and food accessibility (Benchimol and Peres, 2013).

My study subjects also reflect the range of morphological traits evident in omni-frugivores. The largest primate species in my study is the chimpanzee (*Pan troglodytes*) that weighs approximately 50-70kg (Hohmann, 2009). The smallest is the common marmoset (*Callithrix jacchus*) that weighs 260 g (Hohmann, 2009). Most primate species are small-bodied and arboreal as an adaptation to their vital role as seed-dispersers (Chapman et al., 2013). As such, my dataset contains more arboreal primates than terrestrial ones (31 arboreal and 20 terrestrial).

Many omni-frugivore species are omitted from my study due the lack of available data. Therefore my list should not be considered a definitive representation of all omni-frugivore primate species. For instance I omitted *Mandrillus sphinx (*Mandrill) from consideration due to the lack of current research on its diet.

2.2 DATA COLLECTION

2.2.1 DATA CRITERIA

I collected all of my data variables from published literature on primate nutritional ecology. I ran a comprehensive search of primate diets using the academic search engines Google Scholar, JSTOR and PrimateLit Database. I also referred to the bibliographies of papers that I had read. Overall, I compiled 178 academic sources documenting the diets of omni-frugivore primate species.

I used four keywords to find information on the diets of primate species: the primate species name (e.g. olive baboon), diet, large invertebrates and vertebrates. I added a fifth key word for habitat-type (e.g. savannah chimpanzees) to consider primates that exhibit intra-specific variation in habitat preference. I substituted the terms “ecology” or “foraging strategies” for “diet” if the search yielded no results.

I organized the academic sources into three time periods over the past 45 years. I based these time periods on the publication dates: 1970-1984, 1985-2000 and 2001-2015 (see explanation below). Some researchers collected their data a decade before they published their research. In those instances, I classified the data in the decade that the investigator collected it in. I chose the past 45 years for two reasons. During that time, extensive anthropogenic deforestation by heavy machinery occurred (Marsh, 2013). Additionally, more quantitative information on primate diets has been available as technology improved. I used three 15-year increments to make the sequencing between the 45 years consistent. Inconsistent time intervals could have biased any marked change in primate meat consumption. Each time block would have had either more or less time for primate meat intake to change compared to the others. As there was not enough published data to make five-year time increments feasible and 10-year increments left five of the 45-years unaccounted for, 15-year increments were thus the best option.

Hawes and Peres (2013) noted that inconsistent sampling methods have made comparative analyses of literary sources problematic. To account for this problem I followed a number of criteria for a relevant academic source to be included in my study. These criteria are described below.

First, I only included reports on wild primate diets. I did not need to research captive diets since my study is about primate diets in natural settings. I also considered how the investigator recorded the percentage of meat in primate diets. The research had to include the percentage of vertebrates or large invertebrates in the primate diets. If the dietary breakdown mentioned animal matter as a broad category (without specifying the contribution of vertebrates and invertebrates) then the source could not be used.

I did not use research where prey consumption was anecdotal and not quantified.

Furthermore, I consulted literature that used similar sampling methods, in order to be consistent. A majority of the researchers conducted fecal analyses. Some of them also recorded time spent feeding (not foraging) by using group focal-scan sampling. I did not collect research that assessed time spent foraging because time spent foraging does not equate with the contribution of a resource to a primate’s diet (Hohmann et al., 2010). Since primate diets change across seasons, I also used references where investigators conducted their research for a minimum of a year, and differentiated between wet and dry seasons.

I should note that one problem with my study is that I relied upon the research of others. As such, I consider the percentage of meat that the investigators published (and I recorded) as approximated averages to account for intra and inter-observer error.

I also used data on the protein content in plant sources consumed by omni-frugivores.

To find these academic sources I used three key words: “primate species name,” “nutrition,” and the site where the study took place (e.g. Gombe). I used references that assessed the nutritional content of the plants that the primates consumed. I only included the protein content of plant sources that the primates ingested rather than the protein content of all the plant sources found within their habitats. I tried to use the same sites for both meat percentage and protein contents of plants, to account for the variation of protein content in plant sources across sites. Finally, I only considered academic sources where the researcher performed chemical assays on the plants that the primates consumed. For each report I recorded the dry weight of crude protein in the plant sources that each primate species in my study ingested.

2.2.2 DATA STORAGE

I entered the data into a table organized by variable. The sources for the information were recorded on a corresponding copy of the table (found in the Appendices: Appendix 1 and 2). The statistical analysis of the data was conducted using SPSS 20 for Mac.

2.2.3 DATA RECORDING

I recorded nine variables based on the data from published literature: (i) the continent and country in which the primate resides, (ii) habitat, (iii) pattern of locomotion, (iv) meat percentage for the years 2001-2015, (v) meat percentage for the years 1985-2000, (vi) meat percentage for the years 1970-1984, (vii) seasonal preference for consuming meat, (viii) hunting strategy, and (ix) protein content of plant sources. I recorded 560 data points of information (not including null data points). Each variable had specific criteria, which I followed as I entered the data. In the subsequent text, I present the criteria that I used to record the data.

I recorded the continent for each species based on descriptions from academic sources. I used the same articles as those from which I retrieved the meat percentages. For primates that live in multiple countries, I recorded the same continent for the respective species but separated that same species by country. For instance, I recorded two observations for Assamese macaques (*Macaca assamensis)* since they inhabit China and Thailand (Zhou et al., 2014). If data were limited on a species, then I combined two countries together as one observation.

To note the habitat preference for each species I used the descriptions given by each researcher. I also used the same articles to record habitat-types and meat percentages. Overall, I recorded eight habitats attributed to the omni-frugivore species in my sample. While there are more habitat-types used by these species, I could not include them all in my research, as I was limited to a small number of published papers that described habitat-types and percentages of meat consumed. If a species occupied multiple habitats, I recorded each habitat-type for the same species as separate observations. Consequently, particular species studied in more than one habitat-type are represented more than once in my sample. For example, chimpanzees exhibit a range of habitat choices (e.g. woodland, savannah, and tropical wet evergreen forests). Therefore, I recorded three data points for chimpanzees based on their habitat choices. To control for confounding variables, I also recorded the same habitat choice, per omni-frugivore population, for each time period. By doing so, I accounted for intraspecific variation in diets of primates within habitats when I tested across time. I provide broad descriptions of the habitats used in my study in tables 2.1 and 2.2 below.

Table 2.1. Descriptions of omni-frugivore habitats of primate species described in my study

Habitat	Description	Source
Savannah	Savannah habitats are known for their expansive grassland with scattered individual trees. **Temperature**: Temperatures can reach as high as ~38 °C and get as low as ~40 °C. **Seasonality:** Two distinct seasons: ~ seven months dry season and five month wet season. **Precipitation**: There is an average annual rainfall of 76.2-101.6 cm in savannah habitats **Flora**: The dominant foliage consists of forbs (small broad-leaved plants that grow with grasses) and grasses. There are a variety of grass types across savannahs due to differences in temperature and precipitation. **Locations used in my study**: Africa	1
Woodland	Woodland habitats are known for having short trees that are patchily distributed. The region is commonly found surrounded by grasslands, savannah or forested edges. **Temperature**: Woodland temperatures can range from ~10-20 °C **Seasonality**: There are two seasons: ~ five months dry season and ~seven months wet season. **Precipitation**: Woodland can receive 200 to 1,000 mm of rain a year. **Flora**: Shrubs, acacia, chamise, and grasses. **Locations used in my study**: Southwest parts of Africa	2
Tropical Wet Evergreen Forests	Tropical forests are characterized as having greatest diversity of species. **Temperature**: on average 20-25 °C and varies little throughout the year. **Seasonality**: Two distinct seasons: ~ six months dry season and ~six months wet season. **Precipitation**: is even throughout the year and annual rainfall can exceed 2000mm. **Flora:** a high density of species: one square kilometre may contain as many as one hundred different tree species. Trees are 25-35 m tall and mostly evergreen. They can have thick trunks and shallow roots. Plants include bromeliads, vines (lianas), ferns, mosses, palms, and orchids. **Locations used in my study**: Africa, Central and South America, Southeast Asia, Eastern Madagascar, and west coast of India	1
Dry Evergreen Forests	They are similar to tropical wet evergreen forests with the exception that there is a longer dry season (~eight months). **Locations used in my study**: Asia, Central and South America, Africa and Madagascar.	1
Tropical Lowland Karst Forest	Similar to tropical wet evergreen forests, however there are a number of cave formations that increase the acidity of the soil. The permeation of the soil and drainage system (from	3

	the caves) also causes the soil to become dry despite regular rainfall. **Temperature:** ~9.8 °C to 26.6 °C **Seasonality:** four seasons: autumn, winter, spring (where there are monsoon rains) and summer (monsoon rains) **Precipitation**: ~1363mm of rain during the year **Flora:** Karst cave formations contain limestone bedrock cliffs and low valleys. Secondary forests and tropical forest patches surround the low valleys and karst cliffs. **Locations used in my study:** Southern China and Northern Vietnam	
Southeast Asia swamplands	Southeast Asian peat swamplands are a humid wetland environment. It contains standing water that is thick with decaying organic materials (such as dead plants and animals) known as peat. **Temperature:** ~4-22°C **Seasonality:** two seasons: dry and wet seasons. **Precipitation**: ~ more than 2,000 mm of rain annually **Flora:** pond lilies, cattails, sedges, tamarack, and black spruce **Locations used in my study**: Southeast Asia	5
Coniferous Forests	Coniferous Forests have trees that grow needles instead of leaves (the needles remain all year) and cones instead of flowers. This adaptation is beneficial for cold areas. **Temperature:** 40°C to 20°C, average summer temperature is 10°C **Seasonality**: four seasons: long and cold snowy winters (~ five months), spring, summer and autumn. **Precipitation:** 300-900mm of rainfall annually. **Flora**: Pine, spruce and conifer trees. All of these trees contain needles all year long. **Locations used in my study:** Asia and Northern Africa (Morocco).	2
Gallery Forests	Gallery forests are strips of forest that form a narrow corridor along anthropogenic landscapes and/or rivers. These corridors sometimes connect forest fragments to each other. Gallery forests are generally found abutting tropical, dry evergreen or savannah forests. **Locations used in my study:** Madagascar.	4

* **Table 2.1.** All of the above descriptions have been taken from these sources: ***(1)*** The Biomes Group of the Fall 96 Biology 1B class, section 115, at UC Berkeley. (1996). "The Biome Forest Groups" Eds. Pullen, K. Retrieved May 9, 2015 from http://www.ucmp.berkeley.edu/glossary/gloss5/biome/forests.html. ***(2)*** Przyborski, P. (2010). "NASA Earth Observatory: Biomes." Retrieved May 9, 2015 from http://earthobservatory.nasa.gov/Experiments/Biome/index.php/. ***(3)*** Fan, Peng-Fei et al. (2011) Habitat and Food Choice of the Critically Endangered Cao Vit Gibbon (Nomascus Nasutus) in China: Implications for Conservation. Biological Conservation 144(9): 2247–2254. ***(4)*** Seaman, B and C Schulze (2010) The Importance of Gallery Forests in the Tropical Lowlands of Costa Rica for Understorey Forest Birds. Biological Conservation 143(2): 391–398. ***(5)*** Harrison, M et al. (2010) Orang-utan Energetics and the Influence of Fruit Availability in the Nonmasting Peat-Swamp Forest of Sabangau, Indonesian Borneo. International Journal of Primatology 31(4): 585–60.

Table 2.2. Distribution of habitat-types in my study

Habitat	Primate Species	Mean Meat%	Std. Deviation
Savanna	6	2.29	1.560
Woodland	4	2.56	2.640
Tropical Wet Evergreen	22	.95	1.610
Coniferous	3	3.05	4.213
Dry Evergreen	11	1.70	2.978
Tropical Low Karst	1	.00	.
Peat Swamp	3	.04	.051
Gallery Forests	1	.00	.
Total	51	1.43	2.213

I assessed whether a primate was arboreal or terrestrial based on the classifications used by the researchers. If the researcher did not specify the strata use of the primate they studied, I referred to the ICUN Red List database to record the terrestriality or arboreality of the primate (see http://www.iucnredlist.org/search). Some omni-frugivores have the capacity to move between strata over the course of the day. For instance, white-headed lemurs (*Eulemur albifrons*) can spend their mornings in the trees but move to the ground in the afternoon (Vasey, 2005). Researchers identified these omni-frugivores as terrestrial or arboreal based on the area of space (either in a tree or on the ground) most often used. In total, my sample contains 31 arboreal and 20 terrestrial omni-frugivore primate populations. I also recorded the daily path lengths (DPL) of six primate populations from my terrestrial group and six from my arboreal one to discuss the affect of arboreal/terrestrial DPL's on primate meat intake. I retrieved the DPL data from the meat percentage sources with the exception of two primate populations. In those two cases, I used different sources for the DPL but made sure the studies occurred at the meat percentage sites. I only used a total of 12 primate populations for my DPL sample as only twelve sources discussed the DPL of their study species (Appendix 3).

I entered the percentage of meat consumed by the study animals/species from tables of reported diet item percentages in my database. Some authors specified the contribution of vertebrates and invertebrates in their discussion section if the percentage was insignificant to their research question. I classified the percentages of meat for each species into the established time periods mentioned in section 2.2.1.

For the years 2001-2015, I recorded a maximum of three percentages of meat for each primate species and then calculated the mean, which was used for subsequent analyses. The primary reason for recording more than one source in some instances was to account for intra and inter-observer variation across studies. If the data were too limited to allow me to record three percentages of meat, I included as many sources as I could find. For example the Ka'apor capuchin's (*Cebus kaapori*) diet was only recently analysed (see de Oliveira et al. 2014). As such, only one academic source could provide the quantity of meat in the Ka'apor capuchins diet. I did not record a maximum of three percentages of meat for the years 1970-2000 due to limited data and instead recorded one percentage of meat per species.

Since there was a maximum of three percentages of meat per primate species, I labeled each meat percentage as 1, 2 or 3. I then gave the source that provided the information the corresponding number of 1, 2 or 3 (Appendix 1 and 2). I did so to keep track of which academic source provided which meat percentage. I also recorded the study site and habitat for each of the three meat percentages.

If a researcher reported that there was zero consumption of meat by the primate species then I recorded their percentage of meat as zero. In the cases of wet/dry seasons, there were two percentages of meat reported. I used the highest percentage of meat reported and the corresponding season that it was consumed to differentiate between wet and dry seasons.

Recording the meat intake for the years 1985-2000 and 1970-1984 was similar to recording the percentage of meat during the years 2001-2015. I recorded the percentage of meat and the study site where the research occurred. For data prior to 2001-2015, I used articles that presented data from the same sites as the years 2001-2015. If no early research existed on those sites, I used data collected from other sites (as long as the alternative site was in the same country and habitat). In some cases, there were data available for the years 2001-2015 but not for the previous decades. When this occurred, I noted that the percentage of meat for those primate species were non-existent for past decades. When I tested my hypothesis where I question if primate meat consumption has increased over time, I accounted for the non-existent data by excluding those primate species from my sample. Thus to analyse changes in meat intake over time, I used a small sub-sample of the main sample that I used to test the previous hypotheses.

I used the same articles that gave the percentages of meat in the years 2001-2015 to record seasonal preference in meat intake. Since I recorded three percentages of meat per species, there were also three observations of a species' seasonal preference in meat intake. All investigators who examined the same species noted the same seasonal preference per species. So I did not choose one of the three articles over the other to record seasonal preference in meat intake.

I referred to the charts in the articles to record the season in which meat contributed the most to the omni-frugivore's diet. If the investigator concluded that there was an insignificant difference of meat intake between the seasons, I recorded the omni-frugivore as consuming meat during both seasons. I define these hunters as non-preferential hunters as they consume meat with no seasonal preference or pattern. If the primates did not consume any meat then I classified their seasonal preference as null.

Generally, if a species showed intra-specific variation in their seasonal preference for consuming meat then they also lived in two habitats. When this occurred, I separately recorded the variability in seasonal preferences in meat intake with their habitat choice. For instance chimpanzees in Gombe, Tanzania, consume more meat during dry seasons, but Tai forest chimpanzees consume meat during both seasons (Mitani and Watts, 2001). Although the two groups belong to the same species, they live in different habitats: Tai forest chimpanzees in tropical wet evergreen forest and Gombe chimpanzees in woodland habitat (Mitani and Watts, 2001).

I focused on two types of hunting strategies used by my study subjects: "opportunistic hunting" and "cooperative hunting" in addition to the behaviour referred to as "meat sharing." I relied on the researcher's classification of hunting behaviour to record the hunting strategy used by the primate. The understanding of the terms attributed to the strategies (e.g. opportunistic hunting) was generally consistent between researchers, but a small number argued that there are two forms of mutual hunting: cooperative and collaborative. Hamilton (1964), Sussman and Garber (2004) and Strum (2012) argue that hunting is cooperative when the hunters share a common purpose and act together to improve the overall fitness of their group. Sharing a common goal suggests complex social organization and cognitive abilities (e.g. planning ahead) (Strum, 2012). Hunting is collaborative when hunters act together for their own immediate gains, with the benefits to the other hunter a by-product (Boesch et al. 1989; Strum, 2012; Sussman and Garber; 2004). Boesch et al. (2006) offers an alternative view that cooperative hunting is too complex to be made into two distinct types as hunting styles amongst cooperative hunting species are variable; instead cooperative hunting is a reciprocal relationship between the hunters and their group, specific to the social dynamics of the primate species. For instance, male chimpanzees are theorized to use meat as a tool to improve their own rank and attract females while simultaneously providing nutritionally dense food to pregnant females, which benefits the female and her fetus (Stanford, 1996). The struggle with this debate is that the goals of the primate hunters cannot be definitively discerned by researchers, nor are the reasons universal across cooperative hunting species. Despite this debate, most investigators use the term “cooperative hunting”, so I also adopted the term.

I present descriptions of hunting strategies in Table 2.3 because they are the definitions most cited by investigators. If the omni-frugivore did not consume meat then I identified it as a non-hunter. The primate was not considered a meat-sharer if it shared meat only through the act of stealing. According to Gilby et al. (2006), meat sharing requires one animal to give meat to another.

Table 2.3. Hunting Stratagems

Hunting Strategy	Definition	Source
Opportunistic Hunting	When an individual hunts live prey alone with no systematic hunting strategy.	Mitani and Watts, (2001)
Cooperative Hunting	A hunter hunts with companion(s) and has a planned strategy.	Boesch et al., (1994): definition on p. 653
Meat Sharing	The hunter shares meat with an individual who did not catch the prey.	Gilby et al., (2006)

To obtain data on the protein content in plant sources, I primarily used articles that analysed plants consumed at the same sites from which I retrieved the meat percentage. All the literary sources were published after the year 2000 except for two published during the 1990s. I recorded separate observations of protein content for those sampled primate species with data available. I did so to account for variation in morphology, biology and ecology. I also recorded the protein content of plant sources ingested by primates in the season in which their meat intake was the highest.

When a researcher provided the average crude protein of all the plant sources in their study, I recorded the average that they provided. If an investigator published the raw percentage of crude protein in all of the plant sources ingested, without stating the overall average, then I calculated the average myself and recorded the result. The protein content of plant sources was recorded even if the omni-frugivore did not consume meat (e.g. Amazonian squirrel monkey (*Saimiri sciureus)*). When I could not find the protein content of the plant resource via a chemical assay, I recorded the protein content in plant sources as non-existent for that primate.

I did not measure fragmentation rates because there were not enough data available and it has yet to be adequately measured. Therefore I am only analyzing if meat intake increased in tandem with deforestation. Measurements of fragmentation could be useful for further research on the possible relationship primate between meat intake and habitat loss.

2.3 STATISTICAL DATA ANALYSIS

Since the data were pooled together from a number of different studies (and thus researchers), I ran the Shapiro-Wilks test to determine the normality of my sample. The test revealed that the data were not normally distributed (p=0.000) and data points deviated significantly from the line of best fit when plotted on a graph (Figure 2.1). I subsequently used a sequence of non-parametric tests to make comparisons between the independent groups within my sample.

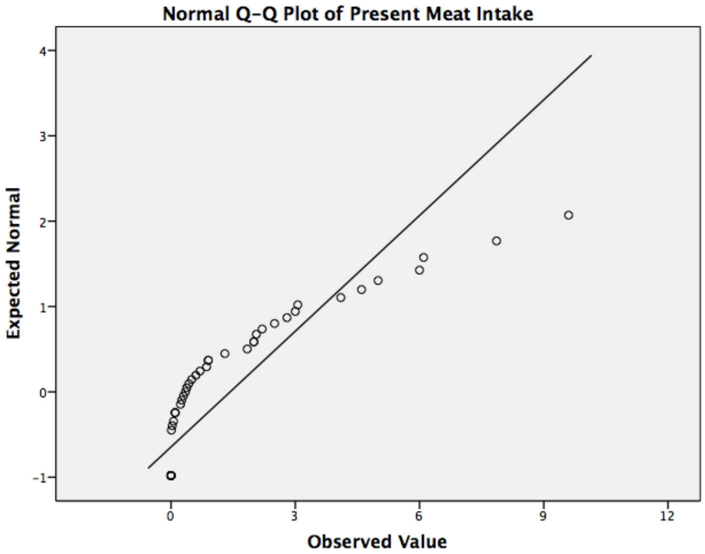

Figure 2.1. The sample's deviation from normality.

As there were three main outliers in my sample (i.e. chimpanzees, common marmosets and capuchins), I also ran a preliminary One-Sample Wilcoxon Rank test to see if the outliers biased my sample. Results indicate that chimpanzees (*U*=72.000, Z=-

5.316, p=0.0001, *N=48*), common marmosets (*U*=39.000, -5.801, p=0.0001, *N=50*), capuchins (*U*=262.000, Z=-3.211, p<0.001, *N=47*), and Barbary macaques (*U*=1.000, Z=-6.169, p<0.000, *N=50*) are significant outliers. As such, I ran each test twice: one without the outliers and one including the outliers. To compare the average between two independent groups I ran the Mann-Whitney-U Test. The benefits of the Mann-Whitney-U Test are that it tests the difference between two distinct groups when the dependent variable is interval and holds the assumption that the data is not normally distributed (Madigral, 2012). I used the Mann-Whitney-U-Test to assess the differences in percentage of meat between strata use, hunting strategies and meat sharing.

I applied the Kruskal-Wallis test when my hypotheses required me to evaluate more than two groups. The Kruskal-Wallis test is thought of as the non-parametric equivalent to a one-way Analysis of Variance (ANOVA) and evaluates the different average means between >3 groups (Madigral, 2012). This test was particularly useful to test my hypotheses because it can be applied when the sample sizes are small and non-symmetrical (Madigral, 2012), two traits which characterized the groups within my sample. I used this test to evaluate the variation in mean meat intake between habitats and seasonal preferences.

Differences in meat intake across time were analysed using the Friedman's test because it determines the difference between the averages of related groups (Madigral, 2012). However, a problem with the Friedman's test is that it only reveals that there is an overall difference between groups and does not infer how isolated pairs of groups differ in relation to one another. Thus, I ran a Post Hoc Wilcoxon test, which identifies the way that groups differ from each other, to calculate how meat intake differs between specific time periods (Madigral, 2012).

For all of the tests, the significant level was set at 0.05 with the confidence interval set at 95%.

2.3.1 Statistical Data Testing

To test for differences in meat consumption relating to arboreality versus terrestriality, the primate species were grouped according to strata-use and tested for overall differences (across continents and habitats). I then separated the arboreal and terrestrial groups of species into their respective continents. The separation enabled me to evaluate which continent potentially contained the terrestrial and arboreal omni-frugivores with the largest discrepancy in meat intake. Similar measures were repeated to test for habitat and seasonal preference in the context of meat intake. When analysing the differences between hunting strategies, meat sharing and plant protein content, I removed the primate species that contained missing data or were not applicable (e.g. non-meat-eating omni-frugivores) in order to run the test. Therefore three of the tests were analysed by using sub-sets of the primary sample that I used to test a majority of the questions. To test meat intake across time, I grouped my sample by time period and then compared the total average percentage of meat in the diets of each time period group (three groups: 1970-1984, 1985-2000, 2001-2015). The same species and sub-species, with the same continental and habitat distributions, were in each time block to account for variability.

2.4 Survey questions

I distributed an international survey to 70 retired and active primatologists to collect more data for my sixth prediction (meat percentage increased in tandem with deforestation). The goal of my survey was to learn if researchers had observed acts of predation by primates at an increased rate over the past 45 years and compare these results those from the literature. The survey contained twelve multiple-choice and five short answer questions (Appendix 5). The primary question was: how many acts of predation have you (the investigator) observed by the primate species that you studied? I made sure that my questions were quantifiable. To quantify the multiple-choice, I provided three options that the primatologist could select from for their answers: less than five predation observations, five to ten observations, or greater than ten predation observations. I wrote the short answer questions as “YES” or “NO” questions. I also split the survey into two parts: short term studies and longitudinal studies. Short-term studies were current studies (to make the data recent) that had a research period of five years or less. Longitudinal studies were more than five years duration and included data conducted before the year 2000 in order to incorporate information before the twenty-first century. To protect the participants, the survey was also designed to be anonymous. After I wrote the survey, I uploaded it onto FluidSurveys to prepare the survey for distribution.

Since the survey involved interacting with people via email, I obtained approval from the University of Victoria’s Human Research Ethics Board to distribute my survey. After I received approval, I contacted board members of primate societies. I asked the board members’ permission to invite their members to take part in the survey. I received responses from the American Society of Primatologists (ASP) and the Primate Society of Great Britain (PSGB). I created a list of ASP participants who studied the diets and nutrition of wild primate populations. I described the objective of the survey, explained the privacy policy, and provided a link to the survey. PSGB members received the same information as ASP members. Both the PSGB and the ASP were given the same time period to complete the survey: March 13, 2015-June 1st, 2015. I closed the survey on June 1st so that the results could be analysed in the summer months. The findings of the survey are reported in chapter three.

CHAPTER 3: RESULTS

3.1 STRATA USE

PREDICTION 1: *I predict that arboreal omni-frugivores include a significantly lower percentage of meat in their diets than terrestrial omni-frugivores. Since the resources within the canopy are diverse (Rose, 1997), arboreal primates can already access an abundance of plants with adequate levels of protein and other nutrients. Therefore, arboreal omni-frugivores do not require meat as a nutritional supplement to the same extent as primates on the ground. I further predict that there is a positive correlation between daily path lengths of terrestrial omni-frugivores and the percentage of meat in their diets. The longer daily path lengths of terrestrial omni-frugivores (Hemingway and Bynum, 2005) may offer more opportunities for prey encounters.*

Overall, terrestrial omni-frugivores in the sample consumed more meat (M =1. 98%, SD= 2.206, N=22) compared with arboreal omni-frugivores (M=1.04% meat, SD=2.170, $N=29$) (Mann-Whitney U-test: U= 180.500, P= 0.007, $N=51$) (Figure 3.1).

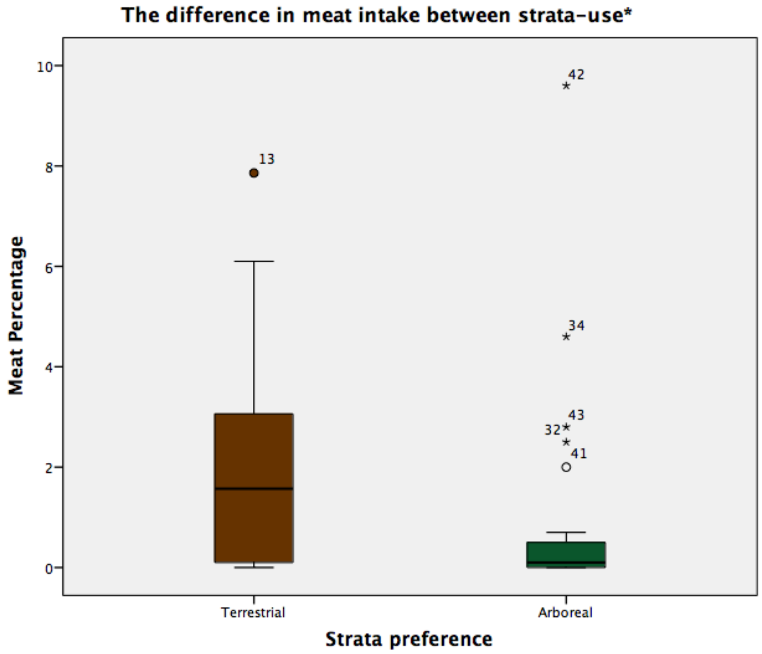

Figure 3.1. The distribution of meat percentages in the diets of terrestrial and arboreal omni-frugivores worldwide. *Brown=Terrestrial and Green=Arboreal.

When I assessed each continent in my sample separately, I found disparities in the amount of meat consumed by terrestrial and arboreal omni-frugivores in Asian (Mann-Whitney U-test: U= 7.500, P= 0.0192, $N=15$) and African (U= 0.000, P = 0.022, $N=15$) countries, whereas I found no differences in the percentage of meat consumed by omni-frugivores between strata levels in the neotropics (*U*=5.00, *P*= 0.857, *N=14*), or Madagascar (*U*=10, *P*=0.229, *N=6*). All but one of the primates in both my neotropical (N: Arboreal =13, Terrestrial =1) and Madagascar samples (N: Arboreal=5, Terrestrial=1) are arboreal, which may account for the divergence from the trend seen on other continents. The two species categorized as terrestrial from the neotropics and Madagascar are not strictly arboreal and spend only 40% of their time on the ground, emphasizing the dominance of arboreality in those samples.

Using a sub-sample of my entire study, I also discovered that terrestrial species in this sub-sample had longer daily path lengths than the arboreal species (Mann Whitney U-test: U= 34.500, *P*=0.004, *N=12*) and that there was a subsequent weak positive correlation between daily path length and meat intake (Spearman's Rank Correlation: $r_s=$ 0.297, *P*= 0.003, *N=12*).

The results described above support my first prediction: that terrestrial primates consume significantly more meat than do arboreal primates worldwide.

3.2 HABITAT PREFERENCE

PREDICTION 2: *I predict that omni-frugivores residing in drier habitats include a significantly higher percentage of meat in their diets than those inhabiting wet-evergreen and deciduous forests.*

The most common habitat-type in my study was wet evergreen forest, which comprised 43% of my sample. The least common types were gallery and lowland karst forests with each comprising 1.8% of my total sample (which are sample sizes that are too small to include in my tests). The species in my total sample that consumed the greatest amount of meat was the common marmoset (*Callithrix jacchus*), which resided in dry evergreen forests.

Overall, the percentage of meat in the diets of omni-frugivores in drier habitats (i.e.

coniferous, woodland and savannah) did not differ significantly from those in wetter habitats (Kruskal-Wallis test: χ^2= 12.897, *P*= 0.075, df=7, *N=51*, Table 3.1).

Table 3.1. Habitat distribution of the primate species in my sample.

Habitat	Wet/Dry	Mean	N	Std. Deviation	Range	Minimum	Maximum
Savannah	Dry	2.29	6	1.560	4	1	5
Woodland	Dry	2.56	4	2.640	6	0	6
Wet Evergreen	Wet	.95	22	1.610	6	0	6
Coniferous	Dry	3.05	3	4.213	8	0	8
Dry Evergreen	Wet	1.70	11	2.978	10	0	10
Tropical Low Karst	Wet	.00	1	.	0	0	0
Peat Swamp	Wet	.04	3	.051	0	0	0.1
Gallery Forest	Wet	.00	1	.	0	0	0
Total		1.43	51	2.213	10	0	10

Thus, prediction two, which suggests that primates in drier habitats consume a significantly higher percentage of meat than primates in wetter habitats, remains unsupported.

Small sample sizes can bias the results of statistical tests, and with this in mind I included a second test where I evaluated only the three habitats that contained the highest number of study species (wet evergreen, dry evergreen and savannah). The average amount of meat consumed by omni-frugivores in wet evergreen, dry evergreen, and savannah habitats varied depending on habitat choice (Kruskal-Wallis test: χ^2=39, *P*= 0.045, df=2, *N=39*). Savannah dwelling omni-frugivores consumed a higher percentage of meat (*M*=2.29%, *SD*= 1.56, *N=6*) compared to the primates residing in the other two habitats (Figure 3.2). As a result, prediction two is supported when dry evergreen, wet evergreen and savannah habitats are considered.

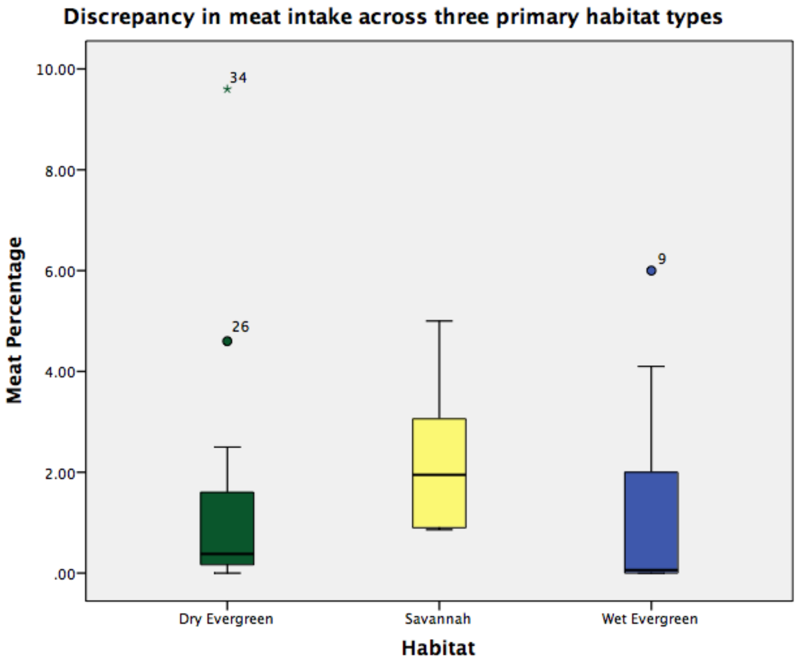

Figure 3.2. The difference in meat intake across the three habitats in my sample that contain the largest group sizes: savannah, dry evergreen and wet evergreen.

3.3 SEASONAL PREFERENCE

PREDICTION 3*: I predict that there is a positive correlation between the percentage of meat in the diets of dry season hunters and the dry seasons associated with seasonal habitats. The reduction in fruit biomass that occurs during dry seasons increases a primate's susceptibility to nutritional deficiency (Ganzhorn et al., 2009). As such, the diets of dry season hunters consist of more meat than those that hunt during wet seasons or both seasons combined. There will also be a greater proportion of dry season hunters to accommodate resource scarcity.*

Omni-frugivores in my study prefer to hunt during dry seasons rather than wet seasons or opportunistically during both seasons. Primate populations that exploit their prey with greater frequency during dry seasons comprise 78% of my hunter sample. Comparatively, 18.9% consume their prey equally in both seasons while 2% of primates catch their prey predominantly during wet seasons. The preference for hunting in the dry season is made more apparent when the distribution of dry season hunters, wet season hunters and both season hunters are observed within their own continents (Table 3.2). In fact, only Africa contained one group of exclusive wet season hunters (a troop of chimpanzees [*Pan troglodytes*] that reside in the Taï Forest of Côte d'Ivoire)

Due to the small sample size of wet season hunters (*N*=1), I ran a single sample against the means test to determine if wet season hunters consumed different amounts of meat compared to dry season hunters. I found that wet season hunters did not consume more meat than did dry season hunters (single sample *t*-test: *t*= 0.13, *P*= 0.990, *N=32*). The remainder of my analysis presented below uses only two variables ([1] dry season hunters and [2] non-preferential hunters) since my sample of wet season hunters is too small to include in statistical tests (*N=1*). Non-preferential hunters hunt with no seasonal preference.

Overall, I found no significant difference in the percentage of meat consumed by dry season hunters, and those that hunt with no seasonal preference (Independent sample *t*-test: *t* = 0.796, *P*=0.432, df=33, *N=37*). I discovered similar results when I analysed the seasonal differences in meat consumption by omni-frugivores within each continent (Mann-Whitney U-test: Africa: *U*=9.000, *P* =0.909, *N=14*; Central and South America: *U*=5.000, *P*= 0.194, *N=14*; Madagascar: *U*=1.000 *P*= 1.000, *N=6*). The omni-frugivores from Asia included in my sample are exclusively dry season hunters and therefore could not be included in the latter test. Thus, part of prediction three, that there are a greater number of dry season hunters compared with wet season hunters, or those with no seasonal preference, is supported. The remainder of prediction three is not supported.

Table 3.2 . Average meat intake differentiated by continent

Seasons	Location	Mean	N	Std. Deviation	Range	Min i\	Max
Dry Seasons	Africa	3.04	10	2.689	8	0	8
	Asia	.05	2	.283	0	0	1
	Central America	2.50	1	.	0	3	3
	Indonesia	.23	5	.277	1	0	1
	Japan Asia	1.65	2	.495	1	1	2
	Madagascar	.15	2	.212	0	0	0
	South America	2.71	7	3.440	10	0	10
	Total	2.17	29	2.535	10	0	10
Both Seasons	Africa	1.96	2	1.556	2	1	3
	Madagascar	.23	1	.	0	0	0
	South America	.79	3	1.064	2	0	2
	Total	1.09	6	1.201	3	0	3
Wet Seasons	Africa	4.55	1	.636	0	5	5
	Total	4.55	1	.636	0	5	5
Overall Total		1.97	36	2.389	10	0	10

3.4 Relationship Between Plant Quality And Meat Intake.

Prediction 4: *I predict that there is an inverse correlation between high protein content in plant resources and the percentage of meat in omni-frugivore diets by continent. Thus, omni-frugivores inhabiting Africa, Madagascar and Asia will exhibit a significantly higher percentage of meat in their diets compared to neo-tropical omni-frugivores because such old world forests contain fewer protein-rich plant sources.*

Using the entire sample (not divided by continent), there was no relationship between the protein content of plants consumed by the sample primates and meat intake (Spearman's Rank Correlation: $r_s = 0.237$, $P = 0.244$, $N=35$, Figure 3.3). The same pattern occurred when I separated my study species by the continents in which they reside with the exception of omni-frugivores from Africa, which exhibited a moderate positive correlation between meat intake and plant protein quality (Spearman's Rank Correlation: $r_s = 0.564$, $P = 0.056$, $N=14$).

I also found no significant relationship between the protein content of consumed plants and meat intake for savannah ($r_s = 0.638$, $P = 0.171$, $N=6$), wet evergreen ($r_s = 0.307$, $P = 0.460$, $N=13$), and dry evergreen residing primates in my sample ($r_s = 0.500$, $P = 0.253$, $N=7$). Nor did I find any discrepancy between the percentage of meat consumed by Old World monkeys in my study and the percentage of meat consumed by New World monkeys (Mann Whitney-U test: $U = 225.500$, $P = 0.473$, $N=33$)

To assess whether any of the outliers affected my results I repeated the above tests without the three outliers from my sample: Barbary macaques, chimpanzees, and common marmosets. Outcomes were similar to my initial ones with the exception of African omni-frugivores. The test run again without using the outliers did not show a positive correlation between protein content in plants and meat intake for African omni-frugivores (Spearman's Rank Correlation, $r_s = 0.036$, $P = 0.936$, $N=10$). Ultimately, prediction four does not hold based on my results.

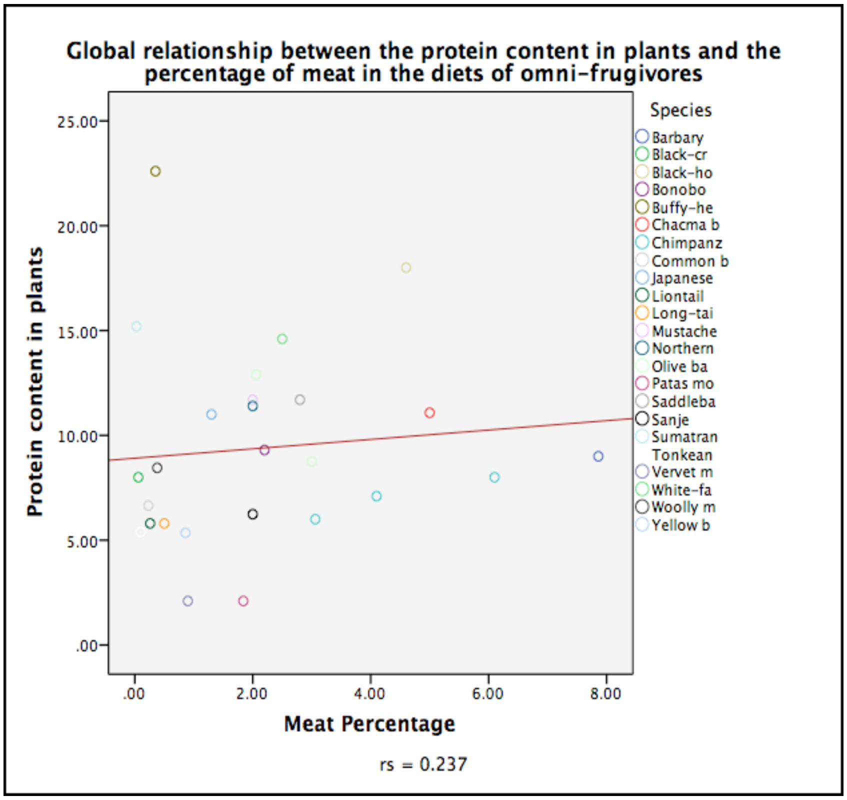

Figure 3.3. The non-significant relationship between the percentage of meat in the diets of omni-frugivores and protein content in the plants consumed by omni-frugivores.

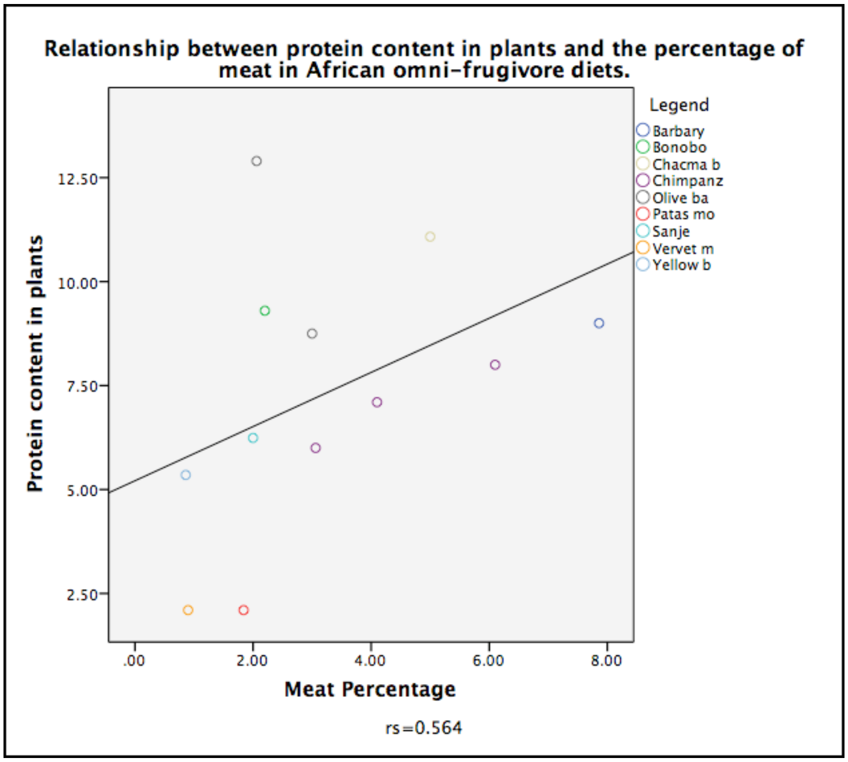

Figure 3.4. The moderate relationship between protein content in plants and meat percentage in the diets of African omni-frugivores.

3.5 HUNTING STRATEGIES AND MEAT SHARING.

PREDICTION 5: *I predict that there is a significantly higher percentage of meat in the diets of cooperative hunters, for example chimpanzees and olive baboons (Papio anubis). Meat-sharers also consume a significantly higher percentage of meat. Cooperative hunting decreases the energy expenditure of one individual through pooled energy, which therefore increases the opportunities for successfully capturing prey and meat sharing (Hohmann, 2009; Strum, 2012; Emery-Thompson, 2013).*

Only 15% of the hunter sample consisted of cooperative hunters while 55% were opportunistic hunters and 30% were non-hunters. Accordingly, opportunistic hunting is a more common hunting strategy utilized by the sampled omni-frugivores. A majority of cooperatively-hunting primate species in my study resided in Africa (e.g. Barbary macaques, baboons and chimpanzees). There are no known New World omni-frugivore cooperative hunters nor are there cooperatively hunting lemurs. With the exception of chimpanzees residing in the Tai Forest, a wet evergreen habitat, the cooperative hunters in my sample resided in savannah, woodland or mountainous regions (N=7); conversely, a substantial number of opportunistic hunters in my study lived in wetter forests (N=13). Cooperative hunters consumed significantly more meat than opportunistic hunters (Mann-Whitney U-test: U=31.000, P= 0.001, $N=35$). The average amount of meat in each diet was 4.01% (SD = 2.262, $N=7$) versus 1.41% (SD=2.133, $N=28$), respectively. Thus, prediction five (cooperative hunters consume a significantly higher amount of meat in their diets) is supported.

All cooperative hunters in my sample also shared meat with troop members. Meat sharing is not exclusive to cooperative hunters however, and some opportunistic hunters in my study were reported to share meat with other group members. Meat-sharers made up 66% of sampled meat eaters and 63% of these meat-sharers were opportunistic hunters. The meat-sharers in my study also consumed more meat (M=2.74, SD=2.585,

$N=20$) than did non-meat-sharers (M=1.20, SD=1.813, $N=12$) (Mann-Whitney U-test: U=67.000, P= 0.0397). As such, the second part of prediction five (meat-sharers consume more meat than non-meat-sharers) is supported by these results.

3.6 CHANGES IN MEAT INTAKE OVER TIME.

PREDICTION 6: *The percentages of meat in omni-frugivore diets have risen significantly in the past 45 years, particularly in areas of human expansion and disturbance. I predict that such an increase has occurred because keystone plant food resources, a former source of protein, have decreased due to habitat disturbance.*

There has been a notable increase in the percentage of meat consumed by the omni-frugivores in my study since the 1970s worldwide (Friedman's test: X^2=17.566, P= 0.000 df=2, $N=36$) (Table 3.3). Between the years 1970-1984, the average amount of meat in the diets of my study species was 0.40% (SD=0.883, $N=36$). The percentage of meat increased considerably to 1.01% (SD=2.028, $N=36$) between 1985-2000. The average percent of meat in an omni-frugivore's diet since the year 2001 is currently 1.59% (SD=2.340, $N=36$)(Figure 3.5 and 3.6). Even the difference in the percentage of meat consumed between time periods (between 1985-2000 and 2001-2015) was significant (Post-hoc Wilcoxon test: P= 0.035, $N=36$).

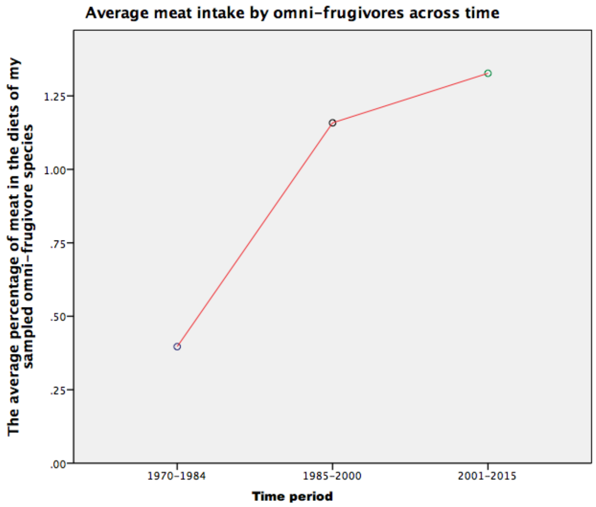

Figure 3.5. The increase in meat intake from 1970-2015 worldwide.

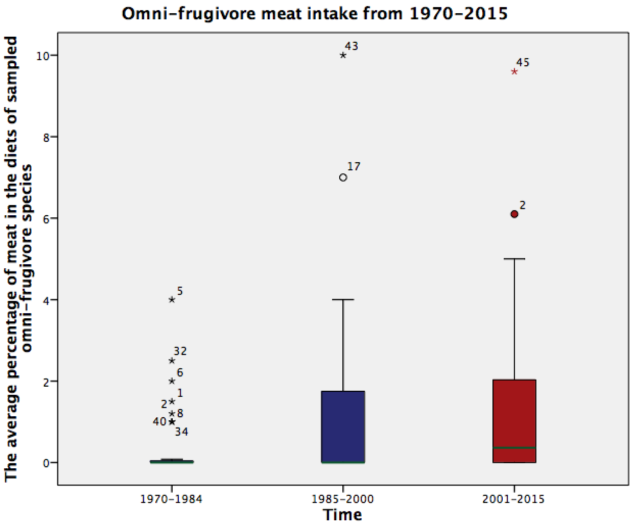

Figure 3.6. The change in meat intake over time depicted as a box plot to emphasize the distribution of each time period group.

The strongest change in percentage of meat in the diets of my study species occurred between 1970-1984 and 2001-2015 (Post-hoc Wilcoxon test: *P*= 0.00029). Overall (i.e. 1970-2014), the South American omni-frugivores in my study displayed the greatest increase of meat consumption (from 0.20% in 1970 to 2.03% at present). The common marmoset, a South American primate, exhibited the greatest increase in meat intake of all species in the sample (increasing 10% between 1970 and 2015).

The group of African primates from 2001-2015 however included a greater total proportion of meat in their diets compared to the diets of primates in other regions. However over this study's total time span (1970-2015), the African sample had a smaller increase in consumption than the South American group. Meat intake by African species in my sample only increased by 0.22% during the years 1970-2000 with a greater spike after the year 2001 by 0.98%. Of all African species in my sample, bonobos (*Pan paniscus*) exhibited the greatest increase in their dietary proportion of meat (2.12%).

Contrasting these results, omni-frugivore meat intake fluctuated across Asia, Central America and Madagascar (Figure 3.6). Within Asia, for example, meat consumption by

Japanese primates in my study actually decreased between 1985 and 2015. Among Central American species in my study, meat intake increased from 1985-2000 but decreased after the year 2001. Overall the average meat intake of Central American omni-frugivores from my sample has remained comparatively high across the three time periods (Figure 3.7). The results presented above support prediction six, that meat intake by primates worldwide has increased since the year 1970. I should again note that deforestation has increased since 1970, though I did not record the data.

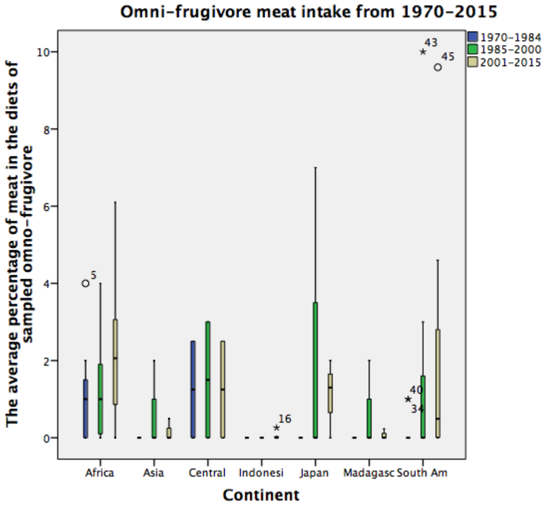

Figure 3.7 The change in meat percentages across time, differentiated by location. Japan and Indonesia are separated from the rest of Asia since both countries are islands with different philosophies on primate conservation (both to mainland Asia and each other). Indonesian omni-frugivores are highly endangered and face a severe degree of deforestation while Japanese macaques have access to monkey centres, which could decrease their meat intake (Hardus et al. 2012; Hanya, 2013)(see chapter four for details).

Table 3.3 The percentage of meat in omni-frugivore diets across time.*

Location	N	Meat % 1970-1984	S.D 1970-1984	Meat % 1985-2000	S.D 1985-2000	Meat % 2001-2015	S.D 2001-2015
Africa	9	1.09	1.326	1.31	1.405	2.29	2.097
Asia	3	0.00	0.00	0.67	1.155	0.17	0.289
Japan	3	0.00	0.00	2.33	4.041	1.10	1.015
Indonesia	5	0.00	0.00	0.00	.06	4.213	0.114
South America	10	0.20	0.422	1.59	3.126	2.03	3.063
Central America	2	1.25	1.768	1.50	2.121	1.25	1.768
Madagascar	4	0.00	0.00	0.50	1.000	0.06	0.115

SD=Standard Deviation.

3.7 SURVEY RESPONSES

I received ten responses from participants to my survey, which was not sufficient to detect any trends. Therefore I did not use the results in my subsequent discussion. I present the results of my survey in Appendix 6, as well as the questionnaire that I distributed to participants (Appendix 5).

CHAPTER 4: DISCUSSION

4.1 RELATIONSHIP BETWEEN STRATA USE AND MEAT CONSUMPTION

Resource Partitioning.

I found no relationship between the protein content in plants and the percentage of meat in omni-frugivore diets. The protein content of plants in the upper crown of a tree is higher than those in the lower strata because increased light availability enables photosynthesis (Brady, 1987; Ganzhorn et al., 1992; Sellin and Kupper, 2005). Therefore, it is unlikely that the low protein values of plants found on the forest floor contributed to the overall higher intake of meat by my terrestrial primate sample. Instead, my results may be partly due to the different food items available to the sampled primates via resource partitioning, which involves the continued use of differing foraging heights by sympatric species.

Resource partitioning reduces agonism and resource competition between sympatric species and conspecifics through the utilization of various food types present within different strata heights (Sing et al. 2011; Zhou et al. 2014). Arboreal primates are more likely to be frugivorous (Hemingway and Bynum, 2005) because they generally prefer to forage at heights of 25-30 metres in the upper portion of the middle canopy and can access a variety of plants (Florchinger et al. 2010). Fruit density can be 4.2 times higher in the upper crown compared with ground level (Houle et al., 2014). Terrestrial primates, on the other hand, exhibit more flexibility in their diets because fruit availability from forest floor plants is not predictably distributed (Hemingway and Bynum, 2005).

Invertebrate density in tropical wet evergreen, dry and deciduous forests can be 2.6 times greater on the ground (Richardson et al., 2005). Fauna are attracted to terrestrial plants, as the hot and windy microhabitat of the upper canopy is not ideal for their survival (Nadkarni et al. 1990). For example, there is a positive relationship between plant size in the terrestrial *Bromeliaceae* tree family and faunal (e.g. beetles, frogs, scorpions) density in the Liquillo Forest, Puerto Rica (Richardson, 1999; Beisiegal et al. 2006). Large invertebrates (e.g. millipedes) also prefer to subsist on decaying wood that falls to the floor, and small vertebrates (e.g. amphibians and small reptiles) consume insects hiding in leaf litter (Kays et al., 2013). It is probable that the high faunal density on the ground provided more opportunities for those terrestrial primates sampled to consume meat. 87% of the terrestrial/semi-terrestrial group were observed extracting large invertebrates and small vertebrates from leaf litter, tree holes and decayed bark. A troop of sampled L'hoest monkeys (*Cercopithecus l'hoesti*), for example, caught 66% of their prey from dead leaves and ground cover (Tashiro, 2006) and the semi-terrestrial bearded capuchin (*Sapajus libidinosus)* from my South American sample, fed in bromeliads (Frietas, 2008).

Marine invertebrates (e.g. molluscs and crabs) and vertebrates (e.g. fish) in particular are also more abundant near the forest floor due to close proximity to water (Stewart et al. 2008; Russon et al. 2014). For instance, male Bornean orang-utans (*Pongo pygmaeus*) catch catfish and snakehead fish from an inland stream in Kaja, an island near Borneo (Russon et al. 2014). Half of the species in my terrestrial sample consume marine prey. The proportion of primates that exploit marine prey and have accessibility to coastal animals may have influenced the trend found in the terrestrial group. However, further research is required to compare the prey encounter rates of my arboreal and terrestrial omni-frugivores samples to verify these claims.

Ranging patterns

Terrestrial omni-frugivores have longer daily path lengths (DPL), larger home ranges and increased foraging times compared to arboreal primates to accommodate the forest floor's low plant density (Hemingway and Bynum, 2005; Kaplin, 2001). Longer DPLs and larger home ranges may account for the trend in the diets of the sampled terrestrial omni-frugivores by increasing their chances of encountering and consuming prey. My results were in line with Gilby et al.'s 2013 study, which found that chimpanzees (*Pan troglodytes*) exhibit a positive correlation between longer daily path lengths and encounters/kills of red colobus (*Procolobus badius*). I found a positive correlation, albeit a weak one, between daily path length and meat intake. Terrestrial omni-frugivores had longer DPL's and ate more meat, whereas arboreal omni-frugivores with shorter DPLs ate less meat. Future research on the correlations between DPLs, frequency of prey encounters and meat percentages is required to determine if DPL is, in fact, related to the trend towards higher meat consumption percentages in terrestrial primate omni-frugivore diets.

Foraging Strategies

The foraging strategies of terrestrial omni-frugivores may have contributed to the high percentage of meat in their diets compared to arboreal ones. Terrestrial primates use extractive foraging to exploit resources that are mixed within leaf litter or found in rotten branches (e.g. seeds, tubers and rotten fruit) (Gibson, 1986; Clymer, 2006; McGraw and Daegling, 2012; Melin et al., 2014). For example chacma baboons (*Papio urisinus*) dig holes in the sand to locate tubers (Clymer, 2006) while chimpanzees probe sticks into tree holes to search for honey (McGrew et al., 2005).

Although there are arboreal extractive foragers (e.g. aye ayes [*Daubentonia madagascariensis*] [Sefczek et al. 2012]), extractive foraging could be linked to high meat intake in the terrestrial group for two reasons. First, extractive foraging increases the opportunities for terrestrial primates to encounter prey, as they are already searching for food in areas of high prey density (i.e. leaf litter) (Gunst et al. 2010; Rothman et al., 2013). For example, chimpanzees probe sticks into holes to extract ants (a process known as ant dipping) (Koops et al., 2015) and bearded capuchins use their fingers to catch caterpillars hiding in the leaves that they are already exploiting (Meulman et al., 2012). Second, primates need to use extractive methods to consume large invertebrates and vertebrates (Gunst et al., 2010). Omni-frugivores must pound marine invertebrates, such as crustaceans and clams, on stones in order to break their shells (Gumert, 2012). They also snatch some invertebrates out of small tree holes, and probe the muscles and sinews from the bone cavities of vertebrates (Milano et al., 2009; Xiang et al., 2013 see examples below).

My data revealed that 61% of the terrestrial omni-frugivore sample is extractive foragers. Some were described extracting meat from shellfish, (e.g. long-tail macaques [Gumert, 2012] and bearded capuchins [Mannu and Ottoni, 2009]) or ripping apart carcasses to access the muscles attached to the bones (e.g. Koshima Island Japanese macaques (*Macaca fuscata*) discard the heads of temperate sea bass and pull the meat from their ribs (Leca et al., 2007]), supporting my argument that extractive foraging contributed to the trend of higher meat consumption by terrestrial omni-frugivores. A potential reason why neotropical and Malagasy omni-frugivores showed no discrepancy in strata-dependent meat intake is that neotropical monkeys and lemurs are predominantly arboreal (my neotropical sample only included one semi-terrestrial species). As such, there were not enough terrestrial omni-frugivores in my neotropical or Madagascar samples to detect any patterns.

4.2 THE EFFECT OF HABITAT ON MEAT CONSUMPTION

4.2.1 GLOBAL SAMPLE

Floristic composition of habitat types

Primate meat intake remained reasonably low for primates in all habitats, countering my prediction that primates in drier habitats consume more meat than those in wetter habitats. One plausible reason is that each habitat provides enough preferred resources for omni-frugivores to consume due to each habitat's unique phenological composition. Consequently, any substantial meat requirements were reduced.

Tropical wet evergreen forests exhibit more heterogeneity than drier ones. They consist of 80% of the world's tree species (200 species per 0.1 hectare) and 50% of its fauna (Singh and Sharma, 2009). As such, tropical forests consist of more edible resources for primates to consume in lieu of meat. Wet forest groups consumed the lowest amount of meat and 81% of sampled non-meat-eaters clustered in wet evergreen forests, which may due to the heterogeneous landscape. For example, southeast dipterocarp forests exhibit mast-fruiting events followed by long periods of low fruit availability (Kanamori et al. 2012). 36% my South Asian omni-frugivore sample accommodate these fluctuations through behavioural adaptations and eating the resources present in dry seasons. They gorge on fruit to gain weight during periods of high fruit abundance and broaden their diets to include the leaves, seeds, and figs available in lean seasons (Hardus et al. 2009; Feeroz, 2011; Schulke et al. 2011; Kanamori et al. 2012). It is therefore possible that South Asian primates have little need for meat, as the resources already present are sufficient. In African wet evergreen forests, Old World monkeys concentrate on young leaves and seeds while New World monkeys in similar neotropical forests, rely on the abundance of sap and fruit available (Stevenson, 2001; Brockman and van Schaik, 2005). In Madagascar, the lack of omni-frugivores in general (due to the relative low fruit density and extreme annual climatic fluctuations) and the reliance on leaves by many that are frugivorous (Ganzhorn et al. 2009), may explain the low quantity of meat ingested by lemurs.

4.2.2 SAVANNAH, WET EVERGREEN AND DRY EVERGREEN SAMPLE

Savannah-dwelling omni-frugivores ingested a greater quantity of meat compared with those in wet evergreen or dry evergreen habitats. Meat eating does not occur more frequently in savannahs during resource scarcity compared with other habitats, nor is meat a significant component of savannah primate diets (Hunt and McGrew, 2002; Bogart et al. 2011).

The data I collected reflects the above research but contrasts in one aspect. Like the above research, the amount of meat ingested by savannah primates was low, which suggests that it is not a critical diet component. Those sampled similarly did not increase their meat intake in dry seasons (see Chapter 3, prediction 4). However, savannah primates ingested more meat compared with those in dry and wet evergreen forests. The greater degree of visibility in savannah habitats could have contributed to this trend. Savannah habitats consist of rocky outcrops, short–statured xerophytic trees (1-20m) and contain a low density of flowering plants) (Isbell and Pruetz, 2007;Alberts, 2007; Riginos and Grace, 2008; Macho, 2014). There is also a negative correlation between tree density and visibility (Riginos and Grace, 2008). Short trees benefit the predatory rates of some savannah primate species (e.g. chimpanzees and baboon spp.) (Uehera, 1997; Hunt and McGrew, 2002) in that reduced canopy provides fewer avenues for prey to escape or hide (Boesch et al. 1994). Chimpanzee hunting success for example, is higher in broken canopies (Mitani and Watts et al. 2002). The mean tree height of habitats occupied by my savannah-dwelling sample is 9.2 m. Comparatively those species in wet evergreen habitats from Africa, Asia and the neotropics have average tree heights of 20 m (Daly and Mitchell, 2000). Therefore, improved visibility in savannah habitats may be a likely cause for the greater meat intake percentage in savannah primate diets.

4.3 THE INFLUENCE OF SEASONS ON MEAT CONSUMPTION

Decline of fruit biomass and nutrient balancing

The lack of nutrients in plant food items leads to increased hunting activity in some primate species (Hladik, 1973; Stanford, 1996; Boesch and Boesch, 2000; Rose, 2001). The trend I observed is consistent with the above-cited research, as 78% of hunters in my sample caught prey more frequently in dry seasons. Resource diversity, nutritional content and abundance during dry seasons partly depend on length: the longer the dry season, the further the nutritional quality and abundance of lianas, epiphytes and plants continues to decline (Hemingway and Byum, 2005). Primates in my neotropical sample in particular are subjected to marked seasonality. The resource abundance in neotropical dry forests decreases from an average 100 kg of fruit per hectare in wet seasons to 40 kg of fruit per hectare in dry seasons (Stevenson, 2005). The neotropical group were correspondingly all dry season hunters.

The fact that meat still constituted a respectively low percentage of all dry season hunter diets (average percentage of total diet: 1.87%) implies that meat is not a critical resource during lean seasons, but rather a nutritional supplement consumed in balanced quantities with fallback foods. Nutrient balancing is the concept that the nutritional goal of foraging is to obtain nutrients in balanced proportions rather than to maximize the profit of any single food component (Rothman and Chapman, 2012; Johnson et al. 2013). Since many primates increase folivory during lean seasons, and young leaves consist of more protein than other flora, protein intake may increase while carbohydrates, fats and micronutrients decrease (Curtis, 2004; Felton et al. 2009; Irwin et al., 2014). Meat provides these calories, macronutrients (e.g. protein and lipids) and micronutrients B6, B12 and zinc (Milton, 2003; Snodgrass, 2009; Tennie et al., 2009). Primates require only a small quantity of meat to fulfil their nutritional requirements, as it consists of high concentrations of these macro and micronutrients (Tennie et al. 2009).

Forest structure: increased visibility during dry seasons

Chimpanzees and white-faced capuchins increase their hunting activity/success in broken canopies: prey that otherwise remain hidden are visible in the sparser foliage and thus encourage these species to hunt (Fedigan 1990; Boesch et al. 1994; Rose 1997). My research suggests a similar pattern. Decrease in crown volume coincides with the reduction of fruit and leaves in forests during dry seasons (Hanya, 2013; Sato et al., 2014; Irwin et al. 2014). 65% of the dry season hunter group reside in wet evergreen and dry evergreen forests, which exhibit the greatest decrease in crown volume (on average 50%) during dry seasons (Estrada-Medina et al., 2013). Furthermore, 85% of dry season hunters hunt opportunistically when prey is in their direct line of sight, and are less inclined to pursue the prey once it scurries into the foliage (e.g. black-crested gibbons

[Fan et al. 2009]; saddle-back tamarins (*Saguinus fuscicollis*) [Nadjafzadeh et al., 2008]). Thus, the dry season hunters in my sample experienced the effects of improved visibility during this period.

4.4 THE RELATIONSHIP BETWEEN PROTEIN CONTENT AND MEAT INTAKE

Diverse food selectivity

The omni-frugivores in my sample (with the exception of African primates) did not consume more meat when the protein content of plants was low; implying that meat consumption is not influenced by plant protein values. There are many factors that influence primate food selectivity besides protein content, including tannin levels, micronutrients, lipid levels, carbohydrate levels and energy (Felton et al. 2009; Johnson, 2012). It is possible that these primates exhibit too much variation in food choice across continents and habitats to detect any substantial trends. Furthermore, hunting may have been too opportunistic to reveal any patterns, for example, red-tailed monkeys (*Cercopithecus ascanius*) from Kibale National Park, Uganda, hunted green pigeons with no predictable pattern (Furichi, 2006) and common brown lemurs (*Eulemur fulvus)* opportunistically preyed on chameleons in the Malaza Forest, Madagascar (Simmen et al. 2003).

In contrast to my prediction and results above, I found that African primates in my sample ate more meat as the protein value in the ingested plants increased, but this may be due to the low number of species considered. My African sample was comprised of only chimpanzees and baboon spp., with an above average percentage of meat in their diet compared to other omni-frugivores (3.25% of total diet). The high meat intake of these species and low protein content of the plants ingested (8.5% protein) may have reduced the difference between these two variables, thus exhibiting a false positive correlation. The fact that I found no trend when I ran the test again without the outliers indicates that these species most likely skewed my result towards a positive correlation and suggests that other African primates followed a similar pattern to primate species on other continents.

4.5 THE EFFECT OF HUNTING STRATEGIES ON PRIMATE MEAT CONSUMPTION

4.5.1 COOPERATIVE HUNTERS VERSUS OPPORTUNISTIC HUNTERS

Energetic cost-benefit ratios

I found cooperative hunters consumed more meat compared with opportunistic hunters, and this result may be related to the profitability of each hunting strategy (cost/benefits of energy). Inter and intra-specific variations in primate foraging strategies are often associated with the energy available in the environment via food sources (Snodgrass et al., 2009; Raichlen et al., 2011). Fruit such as *Dialium aubrevillei* consumed by Diana monkeys (*Cercopithecus diana*) (Eckardt and Zuberbuhler, 2004) are energy-rich but also require energy to exploit as they are patchily distributed. Meat consists of comparatively more energy relative to fruit, and it therefore pays to hunt when the expected meat intake is larger than the cost of hunting the prey (Boech et al.,1994) even though costs include energy expenditure and injury risks (Fedigan, 1990; Boesch et al.,1994; Stanford, 1996; Mitani and Watts, 2001). Opportunistic hunters must rely solely on their own energy to capture prey. Through hunting cooperatively, primates mitigate these energetic costs by pooling their energy together (Packer and Caro,1997; Boesch et al., 2002; Gilby, 2006).

Chimpanzee hunting success is positively correlated with party size (Boesch et al., 2002; Mitani et al., 2002; Tennie et al.,2009). The use of multiple hunters not only divides hunting time and energy requirements in half, but also increases the potential for ambushing the prey (e.g. chimpanzees block the escape routes of red colobus) (Boesch et al., 2002; Gilby et al., 2007; Hohmann, 2009). In contrast, opportunistic hunters (including those I sampled) often lose sight of their prey or are outrun (e.g. white-faced capuchins [Rose, 1997]), increasing their failure rate (Furichi, 2005). The fact that 56% of the opportunistic hunter sample pursue prey in wetter habitats with denser foliage (e.g. peat swamp forest), which impairs visibility, implies that the opportunistic hunters are subjected to these costs while hunting.

The pattern of cooperative hunters residing in savannah habitats may also be related to the energetic costs and benefits of hunting. Longer high-speed chases and stamina are crucial to hunting in savannah plains due to the open nature of the landscape and the characteristics of the prey that reside there (Hohmann, 2009). Savannah prey species are larger than forested ones and adapted towards high-speed running to manoeuvre the open plain and avoid predators (Bro-Jørgensen et al., 2013), for example, Thompson gazelles, exploited by chimpanzees, can reach speeds of 80 km/h (May et al., 2013). Primates in the cooperative hunter group most likely increase their energetic output while hunting these species through including other troop members in their hunt, thus avoiding exhaustion and increasing hunting success. More research is necessary to determine the energy cost-benefits of opportunistic hunters.

4.5.2 MEAT SHARING

100% of my cooperative hunter sample and 63% of my opportunistic group shared meat, and meat sharers ingested more meat compared to non-sharers. Primate food sharing amongst kin and juveniles occurs in some omni-frugivore species (Feistner and McGrew

1989) (e.g. chimpanzees [Boesch et al., 2010] bonobos [Hare et al., 2010], baboon spp., [King et al., 2013] capuchin spp. [Panger et al., 2002]). The benefit of sharing with non-kin however is unclear as the recipient gains fitness benefits at the cost of the donor (Gilby and Stevens, 2003). The 'tolerated theft hypothesis' suggests that food sharing with beggars may avoid the added cost of injury or energy to the hunter (Jones, 1984). For example, black-capped squirrel monkeys (*Saimiri boliviensis*) and chimpanzees are four times more likely to share food with troop members that beg than those that do not, in order to avoid harassment and stealing (Stevens, 2004; Gilby 2006). Meat-sharing in my opportunistic hunter sample is in line with the tolerated theft hypothesis, given that a majority of meat sharing instances occurred after prolonged begging (Gilby, 2006; Hohmann and Fruth, 2008; Palmeira and Pianca, 2008). Additionally, sharing with other hunters may have contributed to the meat-sharing pattern (Jaeggi and van Schaik, 2011).

Meat-sharers also gain reproductive benefits. Male chimpanzees will share with females that are either in estrous or pregnant, a behaviour associated with the meat-for-sex hypothesis (Stanford, 1994b; Mitani and Watts, 2001; Gilby, 2006; Hohmann, 2009). Meat sharing provides reproductive females with extra calories without being subjected to energetic costs or hunting-related injuries (McGrew, 1996; Gombe and Boesch, 2009; Hohmann, 2009). All sampled primates (with the exception of bonobos) exhibited a higher proportion of male hunters compared to females.-Meat-sharers also tended to hunt larger prey relative to their body size while non-sharers hunted smaller prey (Tennie et al., 2009; Jaeggi and van Schaik, 2011). As such, meat-sharers may ingest more meat because they have access to a quantity of meat that can be divided and accordingly shared for the aforementioned benefits whereas non-sharers catch prey that was too small to divide.

4.6 CHANGE IN MEAT INTAKE OVER TIME

Forest Fragments

Forest fragmentation seriously modifies landscapes (Marsh, 2013). Fragmentation creates edges that are more susceptible to the effects of wind and sunlight (Broadbent et al. 2008), which in turn increases primate parasite loads, physiological stress and hinders their degree of survivability (Marsh, 2003; Lenz et al. 2014; Serio-Silvia, 2014). The matrices abutting forest edges are generally agricultural land or open grassland (Pozo-Montuy et al., 2011). Omni-frugivorous primates forced to live in fragments commonly alter their diets to include greater proportions of leaves and non-native plants introduced at the forests edge, or are drawn to anthropogenic foods found within agricultural fields (Estrada, 2012).

97% of meat eaters in the 2001-2015 sample live in fragmented forested habitats with fewer resources and reduced nutritional content compared with the two groups from 1970-2000. Red-tailed guenons in fragmented forests, for example, consume lower amounts of crude protein compared with those in continuous forests (Rode et al., 2005). As I discussed in prediction three, nutritional shortfalls may lead to hunting (Fedigan, 1990; Stanford, 1996; Rose, 1997). The 2001-2015 group may have consumed meat at a higher rate to compensate for nutrient depletion/low fruit abundance in forest fragments, as animal protein provides both macro and micronutrients.

Seven species in my sample living in forest fragments in Asia and South America were noted consuming meat to avoid starvation (e.g. long-tailed macaques [Gunst et al., 2012]. Barbary macaques [Young et al., 2012], Sumatran orang-utans [Hardus et al., 2012), capuchin spp., (Ceballos-Magos and Chivers, 2012]). For example, an inverse relationship was found between low plant-food availability and slow loris consumption in Sumatran orang-utans (Hardus et al., 2012). Primates in my African sample also consumed the greatest amount of meat when all time periods and continents were considered. This finding is likely due, in part, to the fact that Africa consists of lower fruit tree abundance compared with many of the other continents (Sing and Sharma, 2009). Deforestation leading to low fruit abundance may have influenced African primates to adapt their diets to include more meat than those on other continents. Fragmentation may also influence primate meat intake via confined borders and improved visibility. Confined borders reduce home ranges and force primates and their prey species into closer proximity, which therefore increases prey encounters (Sanford, 1996). Chimpanzees at Ngogo National Park are on the verge of causing a local extinction of red colobus due to home range reduction and more frequent hunting of these colobines (Amsler and Watts, 2013). Fragments also improve visibility. Slash and burn agriculture prevents tree regrowth and forces animals to flee while selective logging removes trees that are essential hiding spots, thus making prey easy to spot (Chapman et al., 2006).

Ten primates in my sample that live in fragmented forests have only recently been observed eating meat, which also suggests that the increased meat intake is related to fragmentation (e.g. Barbary macaques [Young et al., 2012]; black-crested gibbons [Fan et al. 2009). For example, Bornean orang-utans were never observed eating meat prior to the 21st century, yet predation events in selectively logged forests have been observed since 2009 (see Russon et al. 2014 and Buckley et al. 2015). Stewart et al. (2008) raised the question of whether new research methods are related to the increase. New technologies such as faecal analyses and camera traps enable detailed observations of primate behaviour and diet. In the case of my study, it is unlikely that these new technologies extensively impacted measures of meat consumption, as 80% of the primate species currently reported eating meat were observed doing so via focal animal sampling, which is the same method used in the 20th Century.

Forest edge and matrix

Forest edges offer more vertebrate prey and potential prey encounters (Lenz, 2014) and some reptile species actually thrive near the forest edges and in human-modified landscapes (Estrada, 2013; Turner, 2012). For instance, white-faced capuchins in a forest fragment near Santa Rosa, Costa Rica, ate more vertebrates than those in the continuous forest (Fedigan and Chapman, 1990), as did saddleback tamarins (*Saguinus fuscicollis*) in northeastern Peru (Kupsch et al., 2014). Of the primates I sampled, 88% are edge-tolerant species (classified by the researchers). These edge tolerant species could potentially consume more prey since they forage at forest edges (see Fig 3.9-3.12, pp 67-68). Actual data is needed, however, to verify my claim. My African sample consisted of primates that consumed the greatest amount of meat overall, and this sample included the greatest number of edge-tolerant species.

The link between forest edges and meat consumption is stronger when crop raiding is considered. Edge-tolerant species are willing to risk navigating in an open matrix in order to consume crops in shaded coffee, palm oil, and eucalyptus plantations in lieu of natural food resources (Estrada, 2013), and prey items can be found here: for example, Tonkean macaques consumed frogs and lizards nested in cocoa leaves (Riley, 2013) and golden-headed lion tamarins (*Leontopithecus chrysomelas*), consumed more prey than the forested group, as bromeliads-planted near their preferred fruit, *Atrocarpus heterophyllus*, attracted frogs, centipedes and beetles (Oliveira et al. 2009). Chimpanzees and capuchins have also been observed leaving forest fragments to hunt livestock (e.g. chickens) within the past ten years (Hockings et al., 2012). Such behaviour infers that domesticated prey becomes accessible through continued modifications of forested landscapes. In sum, this pattern of increased meat consumption may be related to both the increasing forest fragmentation and edge effects. Figures 4.1-4.4 presented on pages 85-86 depict two sites from my study where primates are exposed to edge effects and deforestation.

Pan-Continental Patterns of Fragmentation

I found that increases in meat intake over the three time periods coincide with increases of deforestation worldwide, suggesting a relationship. South America has been the most impacted by such deforestation compared with other countries and continents. From 1990-2005, Brazil alone accounted for 47.8% of global forest loss followed by Indonesia (12.8%) while Africa contributed 5.78% (Hansen et al., 2008). Following World War II, Latin American governments integrated with the global economy (Estrada, 2009) and recognized the monetary value of their resources (e.g. soybean, copper, gold and ore) (Rudel et al. 2009). After 1970, the governments converted to commercial agriculture (Skole et al. 1994), and vast areas have been deforested, e.g. pasture area in Ecuador increased from 2.2 million to 6.6 million ha in 17 years (Masandl et al., 2008). South American primates in my study exhibited the highest increase in meat intake over time (0.20- 2.03%), reflecting such forest loss (Mosandl et al., 2008). The most marked change for sampled South American primates occurred between 1985-2000, following rapid urbanization and the influx of international companies extracting timber, minerals and oil

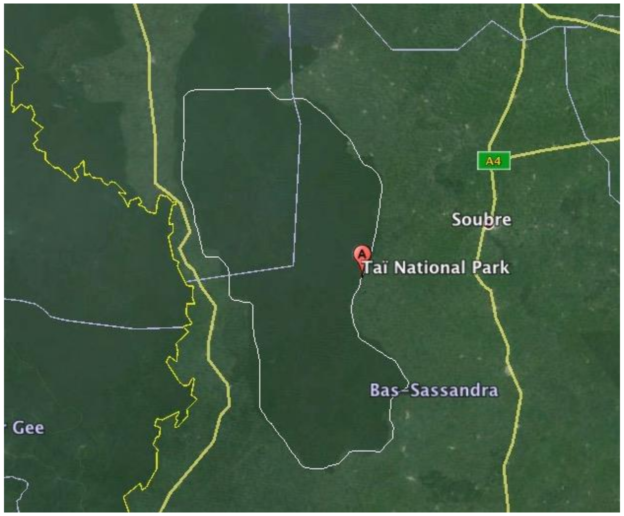

Fig 4.1. Satellite view of Taï National Park Côte d'Ivoire, 2013 (Photo from Google Earth).

Fig 4.2 The edge of the Taï forest and buttressing matrix, indicated by the red square in 1988 (left) and 2015 (right). In 2015 the matrix has been converted to farmland and is larger. Both images to scale at 1132 m. (Photos from Google Earth).

Fig 4.3. Satellite view of Santa Rosa National Park, Costa Rica, 2014. (Photo from Google Earth).

Fig 4.4 A forest fragment in Santa Rosa National Park in 1970 (right), 2002 (centre) and 2014 (right). The red square indicates the forest fragment. A road is visible after 2002 and the forest fragment is visibly smaller. All three images are to scale at 341 m. (Photos from Google Earth

(Rudel et al. 2008; Southgate et al. 2008).

Forest loss in South Asia, particularly in Indonesia, follows South America (Hansen et al., 2008; Jepma, 2014). After 1967, small farms were transitioned to industrial-scale agriculture and converted to palm oil plantations (Haeuber et al., 1996; Lee et al., 2013). Between 2000-2010 over 3,508 hectares of mangrove and peat swamp forests were lost to the palm oil industry (Lee et al. 2013). Indonesian primates consumed the greatest amount of meat between 2001-2015, when deforestation intensified. In contrast to South America, however, meat eating by Indonesian omni-frugivores had never been observed between 1970-2000.

African primates followed the same pattern as South American ones, consistently increasing their meat intake from 1970-2015. During the 1980s, demand from developed countries for commodities such as diamonds, cacao beans and wood, pressured African governments to expand agricultural and timber production, and additionally create 51, 916 km of new roads (Rudel and Ropper, 1996; Laporte et al., 2007 Gibbs et al., 2010). Since 2000, the rate of deforestation has intensified further and is currently four times the world average (Alberts et al. 2014). African governments converted more of the landscape to agricultural farmland (Gibbs et al., 2010) and with land-shortages in Indonesia and Malaysia, multinational agribusinesses and palm oil companies targeted African tropical forests to accommodate rising palm oil exports (Linder et al., 2013; Wich et al., 2014; Abraham et al., 2014). Primates in my African sample ingested the greatest amount of meat during the 2001-2015 time period, which coincides with this palm oil expansion and reliance on agribusinesses (Fitzgerald et al., 2013).

CHAPTER 5: CONCLUSION

Meta-analyses are useful for studying primate conservation because they are starting points for conducting analyses and identifying patterns for future research. Meta-analyses can help assess the effect of a threat to primate sustainability (e.g. loss of a specific fruiting tree species) on a variety of other variables connected to primate conservation (e.g. mortality rates, group sizes and species distribution) and by doing so, narrow down where the threat is acute. One potential study on primate conservation via meta-analysis could involve assessing how the density of fruiting trees and primate species, as well as fragment size, affects primate group size. The results could help discern if there is a tendency for group sizes to be impacted by one factor in particular and consequently, conservation biologists could tailor their research plans accordingly.

My meta-analysis explored the influence of seasons, habitats, resource abundance and anthropogenic forest fragmentation on primate meat consumption. My results demonstrate that meat eating is strongly associated with terrestrial primates, generally more prevalent in drier habitats and seasons, and verifies that the average percentage of meat in omni-frugivore diets increased over the last 45 years. These patterns point toward the conclusion that meat eating may be related to: nutritional stress, resource scarcity and fragmentation. I must emphasize however that as my study was a preliminary meta-analysis, I only found general trends, which require future investigation. For instance, further work should be done to verify if omni-frugivores ingest a greater amount of meat in dry seasons compared to wet seasons. My study indicates that omni-frugivores generally hunt more frequently in dry seasons but I could not discern if they ate greater quantity of meat in dry seasons. Studies on a population level that use fecal analyses to compare the traces of stable isotopes carbon 13 and nitrogen 15 in primate feces between seasons should be conducted in the future. The presence of bone fragments in primate feces would also indicate meat consumption. Such studies would account for variation in primate diets (by focusing on a single primate population rather than making generalizations) when combined with focal animal sampling. Ultimately however, my research best serves as a platform to generate future research on primate conservation by extending one focus of conservation onto meat consumption.

The current state of primate conservation is tenuous. In the past ten years the field of primatology has made some progress in conservation by placing emphasis on studying primates in forest fragments and valuing long-term research studies and local community involvement (Estrada et al., 2012; Shanee et al., 2012; Blanco and Waltert, 2013; Marsh et al., 2013; Salmona et al., 2014; Mugume et al., 2015; Gould and Andrianomena, 2015; Gould and Gabriel, 2015). However conservationists equally face several hindrances to primate sustainability. Some of the long-term effects of fragmentation are now appearing in primate populations and strides in primate conservation are restricted by local socio-economical trends (e.g. lack of funding and illegal bushmeat hunting/logging) (Estrada et al., 2012; Chapman et al., 2013; Marsh, et al., 2013).

Assessing the suitability and sustainability of primate habitats involves considering the relationship between primates and their environment on regional and temporal scales (Chapman et al., 2013). Comparisons of ranging patterns, resource use and the health of primates across time and space can provide valuable insight into ideal habitat conditions or act as warnings to a fragment’s unsuitability (Estrada et al., 2012; Hoffmann et al., 2012; Tesfaye et al., 2013; Behie and Pavelka, 2013; Chapman et al., 2013; Arroroyo-

Rodriguez et al., 2013; Campera et al., 2014). My meta-analysis was one of the first studies to address the relationship between habitat loss and primate meat intake. The pattern that emerged was that meat intake increased over time in areas with forest loss (particuarly South America) or in habitats already vulnerable to resource scarcity (e.g. savannahs). The trend presented here may signify that habitats are becoming increasingly unsuitable for primate sustainability and that primates are including meat in their diets as an adaptation to changing environmental conditions. Therefore, conservation biologists/primatologists should begin to monitor the meat intake of their study species as a marker of habitat degradation (as well as the fact that the inclusion of too much meat could be detrimental to their health [Hohmann, 2009]).

My study was broad and the original data were collected by a variety of researchers. Localized long-term non-invasive surveys (transect surveys) on the temporal changes of both the meat content in the diets of primates and their fragmented habitats, combined with faecal analysis, could provide a fine-grained picture of how or if primate meat intake has changed in the context of fragmentation. Furthermore, these analyses can assess the impact that such a change in diet will cause both ecologically and to local primate populations. Work of this kind could help to understand primate prey-predator dynamics and a habitat's ecological limit at specific population levels instead of the global perspective I took in my meta-analysis. Although meat can act as a nutritional supplement (Fedigan, 1990) and enable ecologically flexible omni-frugivores to proliferate in fragments in the short term (e.g. L'Hoest monkeys [*Cercopithecus l'hoesti*] [Tashiro, 2006]), the increase or introduction of meat in primate diets could disrupt ecological balances (through over exploiting the prey) or indicate that primates are outpacing their resources. One study, by Amsler and Watts (2013), found that chimpanzees (*Pan troglodytes*) in Ngogo National Park, Uganda increased their intake of red colobus (*Procolobus badius)* and concluded that the local population of red colobus will be extinct in ten years. Their focus on meat intake illuminated the impact that meat intake had on both the local populations of chimpanzees (increased border patrols and travel times) and red colobus. The engagement of site-by-site long-term surveys that focus on meat intake thus will assist with tailoring conservation plans that account for variation in resources and prey-predator relationships. Furthermore, long-term surveys on primate meat consumption may also assess if the rise in meat intake is due to data collection bias or new technology, e.g. camera traps and faecal analysis (Leca et al., 2007; Blake et al., 2010; LaFleur et al., 2014), although I believe this is unlikely (as I outlined in 4.6.1).

Literature on primate populations persisting in fragmented forests also suggests the health of such populations is declining and this decline is generally attributed to transmittable diseases and malnutrition (Chapman et al., 2005; Goldberg et al., 2008; Balestri et al., 2014). In the past decade the emergence of transmittable diseases such as Ebola and swine flu has had a devastating impact on primates, particularly great apes (Chapman et al., 2012). Continuous environmental changes and increased proximity between humans and primates promote the likelihood of sharing infectious diseases (Chapman et al., 2012). Genetic similarities between bacteria from humans, livestock and primates also increased three-fold as anthropogenic disturbance within fragments went from moderate to high over time (Chapman et al., 2013). An Ebola outbreak was credited as the cause of death for 25% of the Taï forest chimpanzee population in 1994 (Formenty et al., 1999) and red-tailed guenons from Uganda contracted human-transmitted *Escherichia coli* after habitually entering human settlements to raid crops (Goldberg et al., 2008). Preventative measures have been taken to reduce the chances of transmitting disease, and amendments to primate tourism (i.e. the viewing of wild primates in sanctuaries or nature parks) are being implemented to reduce disease transmission, e.g. some sites have increased the tourist distance from 5m to 10m (Russon and Wallis, 2014).

Meat eating is tied to the transmission of some primate diseases between both humans and other primates (Ragir, 2000; Newton-Fisher, 2015). For Taï forest chimpanzees, the consumption of meat was the highest risk factor for Ebola infection and the risk increased with the quantity of red colobus eaten (Formenty et al., 1999). My findings inferred that meat intake increased with fragmentation and areas already susceptible to disease. As such, my study acts as a potential starting point to observe if meat eating is augmenting primate disease – especially since my data revealed that meat intake is likely rising. Furthermore, close contact between humans, primates and livestock multiplies disease risk (Goldberg et al., 2008) and some of the primate species I sampled consumed meat near the forest edge, or ate livestock and old meat (e.g. chicken) thrown away by tourists or locals from urban centres (e.g. chimpanzees and tufted capuchins [Hockings et al., 2012); long-tailed macaques [Fuentes et al., 2011). Human management of resources is known to have considerable impact on primate behaviour and diets (Chapman et al., 2012; Wich et al., 2012; Wilson et al., 2014). Although no instances of disease were reported in the above-mentioned studies, researchers should consider the implications of where and how tourists deposit unfinished meat products and re-evaluate the proximity of livestock to forest fragments to prevent disease.

In sum, the fact that meat eating-occurred infrequently in the past, and is now becoming more prevalent in areas of habitat degradation, indicates a problem for primate survivability. I was only able to detect general trends in this meta-analysis, it is my hope that more detailed studies at population levels on primate meat consumption are undertaken in order to adequately understand primate nutrition and make strides in conservation by protecting sustainable primate diets in threatened forests.

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Appendix 1. Data Collection

Appendix 1. The data that I used to conduct my analyses *****

Species	Continent	Countries	Habitat	Arboreal or terrestrial	The three percentages taken to receive the average	Average meat percentage 2001-2015	Past meat percentage 1985-2000	Past average meat percentage 1970-1984	Seasonal preference for meat eating	Hunting Strategy	Meat Sharing
Chimpanzees	Africa	Senegal	Savannah	T	1. 0.4% - Fongoli 2. 8%- average from Fongoli and Mt.Assirik 3. 0.8% - Fongoli	3%	1.9% - Mt.Assirik	1.5% - Mt. Assirik	D	C	Yes
Chimpanzees	Africa	Tanzania	Woodland	T	1. Mahale - 7.5% 2. Gombe- 6% 3. Gombe- 5%	6%	3% - Gombe	1.2 –Mahale	D	C	Yes
Chimpanzee	Africa	Uganda and Côte d'Ivoire	TWE	T	1. Ngogo - 3.8% 2. Tai – 7.5% 3. Budongo-1%	4%	2.9% - Ngogo	-	W	C	Yes
Bonobos	Africa	Dem.Repub. of Congo	TWE	T	1. 0%- Kokolopori 2. 3.4% - LuiKotale 3. 2% -Lomako	2%	1% - Lilungu	0.08 - Lomako	D	O	Yes
Chacma baboons	Africa	South Africa	Woodland	T	1. 4% - Southern Cape Peninsula 2. 8% - Loskopdam 3. 3% - Cape Point	5%	4% - Drakensberg	4% - Cape Point	D	C	Yes
Olive baboons	Africa	Kenya	Savannah	T	1. 0.2% - Comoè National Park 2. 2% - Gilgil 3. 4% - Bole	2%	1% - Laikipia	2% - Gilgil Kenya	D	C	Yes
Olive baboons	Africa	Uganda	Woodland	T	1. 3%- Budongo 2. 0% - Kibale 3. 0% - Kaininji	3%	-	-	D	C	Yes
Yellow baboons	Africa	Kenya and Ethiopia	Savannah	T	1. 0% - Filoha 2. 2.5% - Ruaha National Park	1%	0.1 – Amboseli	1% - Amboseli	B	C	Yes

					3. 0.1- Amboseli						
Diana Monkey	Africa	Côte d’Ivoire and Ghana	TWE	A	1. 1.3% – Tai Forest. 2. 0% – Tai Forest 3. 0.6% - Ghana	0%	0% -Tai Forest	0% - Tai Forest	D	O	No
L’Hoest Monkey	Africa	Uganda	TWE	T	1. 5% Kalinzu Forest 2. 0% - Kalinzu Forest	6%	0% -Nyungwe Forest	-	D	O	No
Red-tailed monkey	Africa	Uganda	TWE	A	1. 0% - Kibale 2. 0% - Kibale 3. 0 % - Sabaringo	0%	0% - Budongo	0% - Kakamega Forest	D	O	-
Blue Monkey	Africa	Uganda	TWE	A	-	-	0% - Nyungwe Forest	0% - Kibale	D	O	-
Barbary Macaque	Africa	Algeria	Coniferous	T	1. 0% -Central High Atlas Mountains 2. 11.6 – Akfadou 3. 12% - Ouzoud	8%	0% - Central High Atlas Mountains	0% - Jbel Lakraa	D	O	Yes
Vervets	Africa	South Africa	Savannah	T	1. Bay -0% 2. 0% - Sour Lowveld Bushveld Conservancy 3. 2.7% - Sour Lowveld Bushveld	1%	0.8% - Segera Ranch	0% - Amboseli National Park	D	O	Yes
Patas Monkey	Africa	Cameroon	Savannah	T	1. 2.29% - Kala Maloue Park 2. 3.23% -Kala Maloue National Park 3. 0% Kala Maloue National Park	2%	0% - Kala Maloue National Park	-	D	O	No
Lion-tail macaques	Asia	India	TWE	T	1. 0% - Western Ghats 2. 0.6 – Western Ghats	0%	0% - Western Ghats	0% - Western Ghats	D	O	Yes

					3. 0.2%- Nelliyampathy Reserve Forest						
Japanese macaques	Asia	Japan	Coniferous	T	1. 1% - Yakushima 2. 0.9% – Yakushima 3. 2% - Yakushima	1%	7% - Yakushima	0% - Yakushima	D	0	Yes
Bonnet macaques	Asia	India	DTF	T	1. 0% - Anamalai Hills 2. 0% - Western Ghats 3. 0% - Calicut	0%	0% - Marakkanam Forest	-	-		-
Northern Pig-tailed macaques	Asia	Thailand and Bangladesh	TWE	A	1. 1% - Khao Yai National Park 2. 2% - West Bhangarh Forest 3. 3% - taken from many forested areas in India	2%	0% - Khao Yai National Park	0%- Mentoko Research Centre	D	0	-
Assamese macaques	Asia	China	DEF	A	1. 0% Nong’an National Nature Reserve 2. 0% Nong’an National Reserve 3. 0% - Nong’an National Reserve	0%	-	-	-	-	-
Assamese macaques	Asia	Thailand	DEF	A	1. 2% - Phu Khieo National Reserve 2. 0.1% - Phu Khieo	1%	2.0% - Assam	-	B	O	-
Long-tailed macaques	Asia	Indonesia	DEF	A	1. 0.6 – Telaga Warna, Bogor West Java 2. 0.001% - Padangtegal 3. 0.27 – Mangrove Forest	1%	2% - Kalimantan	0%- Natai Lengkuas	D	O	No

Black-crested macaques	Asia	Indonesia	TWE	T	1. 0% - Tangkoko National Reserve 2. 0.2% – Tangkoko National Reserve 3. 0% - Tangkoko National Reserve	0%	0.0002% – Tangkoko National Reserve	-	D	O	No
Tonkean macaques	Indonesia	Indonesia	TWE	T	1. 0% - Lore Lindu National Park 2. 0% - Lore Lindu National Park 3. 0.4%- Lore Lindu National Park	0%	0%- Lore Lindu National Park	-	D	O	No
Eastern black-crested gibbons	Asia	China	TWE	A	1. 0% - Bangliang 2. 0% - Bangliang	0%	-	-	-	-	-
Western black-crested gibbons	Asia	China	TWE	T	1. 0.3 % - Mt.Wuliang 2. 0% - Mt.Wuliang 3. 0% Mt.Wuliang	0%	0% - Mt.Wuliang	0% - Mt. Wuliang	D	O	-
Javan gibbons	Asia	Indonesia	TWE	A	1. 0% -Gunung Halimun Salak National Park 2. 0% - Citalahab 3. 0% - Ujung	0%	0% - Gunung Halimun Salak National Park	0% - Gunung Halimun Salak National Park	-	-	-
Bornean gibbons	Asia	Indonesia	Peatswamp	A	1. 0% - Sabangau 2. 0% - Barito Ulu Research Reserve 3. 0% - Sabangau	0%	0% -Sabangau	0% - Sabangau	-	-	-
Eastern hoolock gibbons	Asia	China	Lowland Karst	A	1. 0% -Gaoligongshan 2. 0% - Gaoligongshan	0%	0% - Lawachra	0% - Lawachra	-	-	-
Sumatran orang-utans	Asia	Indonesia	TWE	A	1. 0.09% - Gunung Leuser National Park 2. 0.1% - Ketambe	0%	0% - Ketambe National Research	0%- West Langkat Reserve	D	O	Yes

					National Research Centre 3. 0% - Ketambe National Research Centre		Centre				
Bornean orangutans	Asia	Indonesia	TWE	A	1. 0% - Danum Valley 2. 0% - Tuanan Research Station 3. 0% - Sabangau	0%	0% - Gunung National Park	0%- Mentoko Research Site			-
White-faced capuchins	Central America	Costa Rica	DEF	A	1. 3% - Santa Rosa 2 .2% Santa Rosa 3. 2.5% - Lomas Barbudal	3%	3% - Santa Rosa	2.5% - Santa Rosa	D	O	Yes
Ka'apor capuchins	South America	Brazil	TWE	A	1.0.1% - Para State	0%	-	-	D	O	Yes
Tufted capuchins	South America	Brazil	DEF	A	1. 8% - Tijuca Forest 2. 0% - Carlos Botelho State Park 3. 6% - Carlos Botelho State Park	5%	0% - Santa Ganebra Reserve	1% - La Macarena National Park	D	O	Yes
Bearded capuchins	South America	Brazil	Woodland	T	1. 1.1% - Fazenda Boa Vista 2. 1% - Ribeirao das Correias 3. 0.56% – Brazil National Park	1%	-	-	D	O	Yes
Amazonian squirrel monkey	South America	Brazil	TWE	A	1. 0.02% - forest patch near a village of Anaheim 2. 0% - forest patch near village of Anaheim 3. 0% - forest patch near village of	0%	0% - East Amazonia	0% - Parque Nacional Corcovado	B	O	No

					Anaheim						
Geoffroy spider monkey	Central America	Mexico	TWE	A	1. 0% Los Tuxtlas 2. 0% - Refugio de Vida Silvestre 3. 0% Punta Laguna	0%	0% - Santa Rosa	0% - Tikal	-	-	-
Black-faced spider monkey	South America	Bolivia	TWE	A	1. 0% - La Chonta Bolivia 2. 0% - La Chonta 3. 0% - La Chonta	0%	0% -Lago-Caiman	0% - Cocha Cashu, Manu National Park	-	-	-
White-bellied spider monkey	South America	Colombia	TWE	A	1. 0% - Yasunì National Park 2. 0% - Tinigua National Park 3. 0% - Tinigua National Park	0%	0% - Maraca	0% - Amazon Basin	-	-	-
Black lion tamarins	South America	Brazil	TWE	A	1. 0.6% - Caestus Ecological Station	1%	3% – Caestus Ecological Station	1% - Morro do Diabo State Park	D	O	Yes
Mustached tamarins	South America	Costa Rica	TWE	A	1. 3% - Estacion Biologica Quedbrada Blanco 2. 0% - Estación Biológica Quebrada Blanco 3. 2% - Estación Biológica Quebrada Blanco	2%	3% - Manuas Amazonia	0% - Rio de Blanco	B	O	Yes
Saddle-back tamarins	South America	Costa Rica and Peru	TWE	A	1. 5% - Estación Biológica Quebrada Blanco 2. 0% - Forest fragment in North Peru	3%	1.6 – Manuas Amazonia	0% - Rio di Blanco Field Site	D	O	Yes

					3. 3.3% - Estación Biológica Quebrada Blanco						
Common marmosets	South America	Brazil	DEF	A	1. 20% - Tijuca Forest Rio di Janiero 2. 9% -Nisia Floresta 3. 0%- Recife Pernambuco	10%	1. 0% -Nisia Floresta	0% - Cerradao	B	O	No
Buffy-headed marmosets	South America	Brazil	TWE	A	1. 0.7 - Augusto Biological Reserve 2. 0% - Clube de Caça e Pesca Itororó de Uberlândia	0%	1. 10% - Estaco Biologica de Caratinga		B	O	No
Woolly monkey	South America	Costa Rica and Ecuador	DEF	T	1. 1% -Tinigua National Park 1% 2. 0%- Carara Biological Reserve 3. 0.14%- Yasuni National Park	0%	0% - Tinigua National Park	0% - River Caqueta	D	O	No
Common brown lemurs	Madagascar	Northwest Madagascar	Woodland	A	1. 0 % - Mayotte 2. 0.7 -Ankarafantsika National Park	0%	2% - Berenty Reserve	-	B	O	Yes
Collared brown lemurs	Madagascar	Southeast Madagascar	DEF	A	1. 0% - Mandena 2. 0% - Fragment close to the village of St.Luce 3. 0% - Madena	0%	-	-			No
Red ruffed lemurs	Madagascar	Northeast Madagascar	TWE	A	1.0% - Ambatoladama 2. 0% - Masoala Peninsula 3. 0% -	0%	0%- Masoala Peninsula				-

					Ambatoledama						
Black lemurs	Madagascar	Northwest Madagascar	TWE	A	1. 0% - Nosey Faly Peninsula	0%	0% - Ambato Massif	-	-		-
Blue-eyed black lemurs	Madagascar	Northern Madagascar	DEF	A	1. 1% - Ankarafa Forest 2. 0% - Ankarafa Forest 3. 0% - Ankarafa Forest	0%	-	-	B	O	-
Ring-tailed lemurs	Madagascar	Southern Madagascar	Spiny forest	T	1. 0% - Berenty Reserve	0%	0% - Beza Mahafaly Reserve	-	-	-	-
Ring-tailed lemurs	Madagascar	Southern Madagascar	Gallery forests	T	1. 0% - Berenty Reserve 2. 0% - Berenty Reserve 3. 0%- Beza-Mahafaly Reserve	0%	0% - Berenty Reserve	0%- Berenty Reserve	-	-	Yes

Appendix 1- TWE= Tropical Wet Evergreen; DTF= Dry Evergreen Forest; C= Cooperative Hunting; O=Opportunistic Hunting; D= Dry Season; B=Both Seasons; T= Terrestrial; A= Arboreal

Appendix 2. Data Collection Sources

Appendix 2. The academic sources that provided my data

Species	The three percentages taken to receive the average	Past average meat percentage 1985-2000	Past average meat percentage 1970-1985
Chimpanzees	1.Bogart (2009) 2.Bogart et al. (2011) 3.Pruetz et al. (2006)	1. McGrew et al. (1988)	1. McGrew et al (1983) cited IN Pruetz (2006)
Chimpanzees	1.Matsumoto-Oda (2002) 2.Pruetz et al. (2006) 3.Plummer et al. (2000)	1. Gombe Research Centre and McGrew (1992) cited In Stanford (1996)	1. Takahata et al. !984) cited IN Pruetz et al. (2006)
Chimpanzee	1.Emery-Thompson et al. 2008 2.Fahy et al. (2013) 3.Head et al. (2011)	1.Wrangham et al. (1991)	-
Bonobos	1.Georgiev et al. (2011) 2.Beaune et al. (2013) 3.Conklin et al. (2001)	1. Bermejo et al. (1995)	1. Badrian and Badrian (1981)
Chacma baboons	1.Van dorn et al. 2010 2.Codron et al. 2006 3.Kamilar et al. (2002)	1. Whiten et al. (1987) cited IN Byrne and Whiten (1991)	1. Davidige cited IN Hill and Dunbar (2002)
Olive baboons	1. Kunz et al. (2008) 2. Kamilar et al.(2002) 3. Hill et al. (2002)	1.Barton et al. (1990)	1. Harding et al. (1976)
Olive baboons	1. Okecha et al. (2006) 2. Johnson et al. (2012) 3. Adeola et al. (2014)		
Yellow baboons	1. Swedell et al. (2007) 2. Pochron et al. (2000) 3. Alberts et al. (2005)	1. Alberts et al. (1996)	1. Post (1981)
Diana Monkey	1. Buzzard et al. (2006) 2. Ekhardt et al. (2003) 3. Curtin (2002)	1. Watcher et al. (1997)	1. Li and Henry (1991)
L'Hoest Monkey	1. Tashiro (2006). 2. Tolo (2008)	1. Kaplin (2001	
Red-tailed monkey	1. Chapman et al. 2013 2. Stickler (2004)	1. Tweheyo and Obua (2001)	1. Cords et al. (1986)

	3. Bektic (2009)		
Blue Monkey	1 .Tesefye et al. (2013) 2. Fairgrieve et al. (2003)	1. Kaplin et al. (1998)	1. Butynski et al. (1990)
Barbary Macaque	1. El Alami et al. (2012) 2. Hanya et al. (2011) 3. El Alami and Chait (2012)	1.Menard et al.. (2002)	1. Melhman et al. (1988)
Vervets	1. Tournier and Tournier (2014) 2. Barrett (2005) 3. Pruetz and Isbell (2000)	1.Pruetz et al. (2000)	1.Wrangham and Waterman (1981)
Patas Monkey	1. Nakagawa (2003) 2. Nakagawa (2000) 3. Nakagawa (2007)	1.Nakagawa (1989)	-
Lion-tail macaques	1. Sing et al. (2011) 2. Kumara et al. (2000) 3. Eringey et al. (2014)	1.Singh et al. (2000)	1.Green et al. (1977)
Japanese macaques	1. Hanya et al. (2004) 2. Hanya et al. (2003) 3. Hanya et al. (2011)	1.Hill et al. (1997)	1. Arushal et al. (1980)
Bonnet macaques	1. Johnson et al. (2007) 2. Sing et al. (2011) 3. Dileep et al. (2013)	1.Krishnamani (1994)	1. Lindenburg et al. (1980)
Northern Pig-tailed macaques	1. Albert et al. (2013) 2. Feeroz (2011) 3. Feeroz (2012)	1.Whitington et al. (1992)	1. Berenstain (1986)
Assamese macaques	1 . Huang et al. (2014) 2. Zhou et al. (2011) 3. Zhou et al. (2014)	-	-
Assamese macaques	1. Schulke et al. (2011) 2. Richter et al. (2014) 3. Iy Ne et al. (2004)	1.Srivastava (1999) IN Richter et al. (2010)	-

Long-tailed macaques	1. Nila et al. (2014) 2. Fuentes et al. (2011) 3. Gumert et al. (2012)	1. Wheatly et al. (1996)	1. Yeager et al. (1996)
Black-crested macaques	1. Sumarto et al. (2010) 2. Giyarto (2012) cited IN Richter (2014) 3. Suprinata et al. (2008)	1.O'Brien et al. (1997)	1. Richard et al. (1989)
Tonkean macaques	1. Riley et al. (2013) 2. Riley et al. (2007) 3. Riley (2007)	1.Pombo et al. (2004)	1. Richard et al. (1989)
Eastern black-crested gibbons	1. Fan et al. (2012) 2. Fan et al. (2011)	-	-
Western black-crested gibbons	1. Fan et al. (2009) 2. Fan et al. (2010) 3. Xiao et al. (2009)	1. Lan (1993)	1. Haimoff et al. (1987)
Javan gibbons	1. Kim et al. (2010) 2. Kim et al. (2012) 3. Elder (2009)	1. Malone et al. (2007)	1. Kappelar et al. (1984)
Bornean gibbons	1. Cheyne (2010) 2. McConkey (2003) 3. Elder et al. (2009)	1. McConkey (2002)	1. Rodman et al. (1978) IN Sailer et al. (1985)
Eastern hoolock gibbons	1. Fan et al. (2013) 2. Zeung et al. (2014)	1. Islam (1992)	1. Tilson et al. (1979)
Sumatran orang-utans	1. Hardus et al. (2012) 2. Hardus et al.(2009) 3. Russon et al. (2009)	1. Ungar (1995)	1. MacKinnon (1974) cited IN Wheatly (1982)
Bornean orangutans	1. Kanamori et al. (2010) 2. Vogel et al. (2009) 3. Harrison et al. (2010)	1. Knott (1998)	1. Leighton (1993)
White-faced capuchins	1. MacKinnon et al. (2004) 2. Pers. Communication from Rose and extrapolated	1. Rose (1994)	1. Chapman and Rose (1990)

	IN Watts et al. (2005)		
Ka’apor capuchins	1. de Oliveira et al. (2014)		
Tufted capuchins	1. Cunha et al. (2006) 2. Izar et al. (2004) 3. Izar et al. (2012)	1. Galetti (1994)	1. Izar (1978) cited IN Fragaszy (2004)
Bearded capuchins	1. Verdane et al. (2013) 2. Frietas et al. (2008) 3. Sabbatini et al. (2008)	-	-
Amazonian squirrel monkey	1. Lima et al. (2002)- just divided from obs. 2. Stone et al. (2007) 3. Stone et al. (2008)	1. Souza (1997)	1. Boinski (1987)
Geoffroy spider monkey	1. Garcia-Ordun (2002) in Gonzalez-Zamora et al. (2009) 2. Hernandez and Stone (2005) 3. Ramos Fernandez et al. (2003)	1. Chapman (1988)	1. Cant (1990)
Black-faced spider monkey	1. Felton and Felton (2010) 2. Felton and Felton et al. (2009) 3. Felton et al. (2008)	1. Wallace (2005)	1. White (1986)
White-bellied spider monkey	1. Suarez et al. (2006) 2. Stevenson and Link. (2010) 3. Link et al. (2006)	1. Nunes (1998)	1. Izawa (1975)
Black lion tamarins	1. Keuroghlian and Passos (2001)	1. Passos (1999) IN Kleiman and Rylands (2002)	1. Valladares-Padua (1993) cited IN Kleiman and Rylands (2002)
Mustached tamarins	1. Nadjafzadeh et al. (2008) 2. Culot et al. (2010) 3. Kupsch et al. (2014)	1. Peres (1993)	Garber (1988)
Saddle-back tamarins	1. Nadjafzadeh et al. (2008) 2.Porter et al. (2013) 3. Kupsch et al. (2014)	1. Peres (1993)	1. Garber (1988)
Common marmosets	1. Cunha et al. (2006) 2. Digby (2011) –unpublished data 3. Schiel et al. (2010)	1. Castro and Araujo (2006)	1. De Fonesca et al. (1984)

Buffy-headed marmosets	1. Hilario et al. (2010) 2. Vilela et al. (2011)	1. Ferrari (1988)	-
Woolly monkey	1.Stevenson et al. (2006) 2. Stevenson and Gonzalez (2014) 3.DiFiore (2004)	1. Peres (1994)	1. Izawa (1975)
Common brown lemurs	1. Tarnaud et al. (2004) 2. Sato et al. (2014)	1. Simmen et al. (2003)	-
Collared brown lemurs	1. Donati et al. (2011) 2. Donati et al. (2007) 3. Serra et al. (2012)		
Red ruffed lemurs	1.Martinez et al. (2010) 2. Dutton et al. (2008) 3. Martinez and Razafindratsima (2014)	1.Vasey (2000)	-
Black lemurs	1. Simmen et al.2007	1.Coloquhoun (1993)	-
Blue-eyed black lemurs	1. Valempelo et al. (2013) 2. Valempelo et al. (2011) 3. Schwitzer et al. (2007)	-	-
Ring-tailed lemurs	1. Gould et al. (2011)	1.Yamashita (2002)	-
Ring-tailed lemurs	1. Yamashita et al. (2008) 2. Simmen et al. (2006)	1.Simmen et al. (2003)	1. Pinkus et al. (2006)

Appendix 3. Comparison of the daily path length of some arboreal and terrestrial omni-frugivores in my sample and meat intake

Species	Continent, Country	Arboreal/Terrestrial*	Daily Path Length (DPL)	Meat Percentage	Source
Chacma baboons (*Papio ursinus*)	Cape Peninsula, South Africa	Terrestrial	4.67 km	4%	Hoffman and O'Riain, 2011
Chimpanzees *(Pan troglodytes)*	Kibale National Park, Uganda, Africa	Terrestrial	5 km	3.8%	Chapman and Chapman, 2000
Chimpanzees	Tai Forest, Côte d'Ivoire, Africa	Terrestrial	2.4 km	7.5%	Doran, 1996
Diana monkeys (*Cercopithecus diana*)	Tai Forest, Côte d'Ivoire, Africa	Arboreal	1.125 km	1.06%	Buzzard, 2006
Red-tailed monkeys (*Cercopithecus ascanius)*	Kibale National Park, Uganda, Africa	Arboreal	1.111 km	0%	Stickler, 2004
L'hoest monkeys (*Cercopithecus l'hoesti)*	Kibale National Park, Uganda, Africa	Terrestrial	2.092 km	2.5%	Buzzard, 2006
Yellow baboons (*Papio cyncephalus)*	Issa, Tanzania	Terrestrial	4.7 km	1%	Johnson et al. 2015
Assamese macaques (*Macaca assamensis)*	Phu Khieo National Reserve, Thailand	Arboreal	0.604 km	1%	Richter et al. 2015
Japanese macaques *(Macaca fuscata)*	Northern Alps, Japan	Terrestrial	2.0 km	2%	Izumiyama et al. 2003
Blue-eyed black lemur (*Eulemur flavifrons)*	Ankarafa Forest, Madagascar Masoala Peninsula, Madagascar	Arboreal	0.645 km	0%	Volampeno et al. 2011
Red-ruffed lemurs (*Varecia variegata rubra*)	Punta Laguna, Mexico	Arboreal	0.1279 km	0%	Rigamonti et al. (1993)
Geoffroy's spider monkey (*Ateles geoffroyi)*		Arboreal	0.1182 km	0%	Ramos-Fernandez et al. 2003

Appendix 4. Protein Content of Plants Data Collection

Species	Location	Habitat	Protein Content of plants ingested	Source
Bonobos	Solanga Park, Central Africa	Savannah	6	Hohmann et al. (2012)
Chimpanzees	Kibale National Park, Uganda, Africa	Wet Evergreen	7.1	Houle et al. (2014)
Chimpanzees	Gashaka, Nigeria, Africa	Woodland	8	Hohmann et al. (2010)
Bonobos	Lui Kotale, Central Africa	Wet Evergreen	9.3	Beaune et al. (2013)
Chacma baboons	Cape Peninsula, South Africa	Savannah	11.08	Johnson et al. (2013)
Olive baboons	Lakipeia, Uganda, Africa	Savannah	12.9	Barton and Whiten (1994)
Olive baboons	Kainji, Nigeria, Africa	Woodland	8.75	Adeola et al. (2014
Yellow baboons	Africa Lakipeia, South Africa	Savannah	5.35	Macho (2014)
Diana monkeys	Taï National Park Côte d'Ivoire	Wet Evergreen	9.5	Hohmann et al. (2010)
L’hoest monkeys	Udzungwa Mountains, Tanzania, Africa	Wet Evergreen	6.24	McCabe et al. (2013)
Red-tailed guenons	Kibale National Park, Uganda, Africa	Wet Evergreen	17.6	Conklin-Brittain et al. (1998)
Blue monkeys	Kibale National Park, Uganda, Africa	Wet Evergreen	17.6	Conklin-Brittain et al. (1998)
Barbary macaques	Kinzazan, North Africa	Deciduous Forest	9	Hanya et al. (2011)
Vervet monkeys	Laikapia, Kenya, Africa	Savannah	2.1	Isbell et al. (2013)

Patas monkeys	Laikapia, Kenya, Africa	Savannah	2.1	Isbell et al. (2013)
Liontail macaques	Kerala, India	Wet Evergreen	5.8	Krishnadas et al. (2011)
Japanese macques	Yakushima, Japan	Coniferous	11	Hanya et al. (2011)
Northern pig-tailed macaques	Kon Ka Kinh, Vietnam	Wet Evergreen	11.4	Tinh et al. (2012)
Black-crested macaques	Sulawesi, Indonesia	Tropical Forest	8	Riley et al. (2013)
Tonkean macaques	Sulawesi, Indonesia	Tropical Forest	5.39	Riley et al. (2013)
Sumatran orang-utans	Sumatra, Indonesia	Tropical Forest	15.2	Hamilton et al. (1994)
Bornean orang-utans	Borneo, Indonesia	Tropical Forest	9.64	Knott et al. (1998)
White-faced capuchins	Santa Rosa, Costa Rica, South America	Dry Forests	14.6	McCabe et al. (2007)
Tufted capuchins	Suriname, South America	Dry Forest	18	Boinski et al. (2000)
Tufted capuchins	Caatina, South America	Woodland	18	Emidio et al. (2012)
Geoffroy’s spider monkey	Mexico, Central America	Tropical Forest	12.35	Ganzhorn et al. (2009)
White-bellied spider monkey	Bolivia, South America	Tropical Forest	24	Felton et al. (2009)
Mustached tamarins	Peru, South America	Tropical Forest	11.7	Smith et al. (2000)
Saddle-back tamarins	Peru, South America	Tropical Forest	11.7	Smith et al. (2000)
Common marmosets	Venuzuala, South America	Dry Forests	27	Norconk et al. (2009)
Buffy-headed marmosets	Brazil, South America	Tropical Forest	22.6	Hilario et al. (2011)
Wolly monkey	Preu, South America	Dry Forests	8.45	Norconk et al. (2009)
Common brown lemurs	northwestern Madagascar	Scrub	6.65	Sato et al. (2014)
Collared lemur	Saint Luce, southeast Madagascar	Littoral Forest	6.5	Donati et al., (2007)

Blue-eyed black lemur	Nosy Faly Peninsula, norwestern Madagascar	Tropical Forest	10.09	Simmen et al., (2007)
Ring-tailed lemurs	Berenty Reserve, southern Madagascar	Spiny	20.72	Gould et al. (2011)
Ring-tailed lemurs	Beza Mahafaly, southwestern Madagascar	Gallery	15.6	Yamashita (2008)

Appendix 5. Survey Questionairre Template

* Survey was used but an inadequate number of responses were received to include in the main thesis.

Sample Survey Questionnaire

A cross-comparative analysis, across continents, of meat consumption in omnivorous-frugivorous primates

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Emma Blinkhorn

Abstract

The survey below contains questions about the predation of large invertebrates and vertebrates by omnivorous-frugivorous primates. Non-human primates do not characteristically include large proportions of large invertebrates and vertebrates in their diet. The aim of my research is to evaluate if the percentage of meat in the diets of omni-frugivores has increased in the twenty-first century. My secondary objective is to assess if this is correlated with anthropogenic deforestation. Subsequently, the purpose of this survey is to determine if primatologists are observing increased predation by the primates at research sites.

Disclaimer and Privacy Policy

Access to your information: This survey will be conducted through the Canadian program FluidSurveys and the data will be stored in a Canadian server. Since this survey is anonymous your private information will remain confidential and not shared with the primary investigator (EB) or others. However, FluidSurveys recently partnered with the American program SurveyMonkey as of July 14, 2014. Thus, even though the data is stored in a Canadian server, the responses you give in the survey might be accessed via the U.S Patriot Act.

Anonymity: The survey will be anonymous and I will not be able to connect your responses to others. *You do not need to give out any personal information while answering the questions or leave your name*.

Future Use: The primary researcher (Emma Blinkhorn) might revisit the question raised in this study (has the percentage of meat in the diets of omni-frugivores increased?). As such, the responses collected in this survey might be used in the future.

Right to withdraw: Please note that you have a right to withdraw from this study at any time and can request to have your answers removed.

Voluntary participation: You have a right to answer the questions of your choosing and can leave some answers blank.

If you are agreeable to the possibility that the U.S government might access your responses and consent to future use of this survey, please sign the consent form below before you complete the survey.

Consent Form

(1) Please be advised that this research study includes data storage in the U.S.A. As such, there is a possibility that your responses gathered for this research study may be accessed without your knowledge or consent by the U.S. government in compliance with the U.S. Patriot Act. University of Victoria Ethics Committee.

<u>Statement of Consent</u>*:* I agree with this disclaimer and have been advised that my responses for this research study could be accessed in the future by the U.S government without my consent. ☐

(2) Please be advised that the responses that you give in this survey might be used in the future by the primary investigator (Emma Blinkhorn)

Top of Form

<u>Statement of Consent:</u> I have read the above disclaimer and understand that the responses that I give in this survey might be used in the future by the primary investigator (Emma Blinkhorn) ☐

Part 1.

1.1 Definitions of terms used in this survey:

Large invertebrates: animals such as mollusks, crabs and millipedes (McGrew, 2014).
Vertebrates: small to medium sized mammals, reptiles, amphibians and birds (McGrew, 2014)
Cooperative Hunting: A series of individuals that work together to catch prey that has been sighted (Strum 2012): 17
Meat Sharing: The hunter shares meat with an individual who did not catch the prey (Hohmann 2009):9.
Opportunistic Hunting: The spontaneous consumption of live prey by a hunter with no systematic strategy for hunting it (Mitani et al. (2001): 917.

1.2 Please state which primate species you study and the site where you conduct your research:

1. Primate species (please state all the primate species that you study if applicable):

   ____

2. Please state your research site (s):

   ____

Part 2.

The following questions are applicable if your research is longitudinal and contains data prior to the year 2000. If your research does not include data that was collected at any point from 1970 to 1985 then please forgo questions 3, 4 and 5.

1. In the years spanning 2001-2015 have you noticed

i. No large invertebrate and vertebrate predation by the primates that you research.
ii. Less than five sightings of large invertebrate and vertebrate predation by the primates that you research.

iii. Five sightings of large invertebrate and vertebrate predation by the primates that you research.

iv. Ten or more sightings of large invertebrate and vertebrate predation by the primates that you research.

2. If you have noticed ten or more sightings of large invertebrate and vertebrate predation at the site where you conduct your research, please specify an approximate number if possible:

______________________________.

3. In the years spanning from 1985-2000 did you notice:

i. No large invertebrate and vertebrate predation by the primates that you research.

ii. Less than five sightings of large invertebrate and vertebrate predation by the primates that you research.

iii. Five sightings of large invertebrate and vertebrate predation by the primates that you research.

iv. Ten or more sightings of vertebrate predation by the primates that you research.

4. Is the data that you collected in the periods of 2001-2015 and 1985-2000 from the same research site?

i. Yes
ii. No

5. In the years spanning from 1970-1985 was there:

i. No large invertebrate and vertebrate predation by the primates that you research.

ii. Less than five sightings of large invertebrate and vertebrate predation by the primates that you research.

iii. Five sightings of large invertebrate and vertebrate predation by the primates that you research.

iv. Ten or more sightings of large invertebrate and vertebrate predation by the primates that you research.

6. Throughout the course of your research, has the type of large invertebrate and vertebrate prey that the primates exploit changed over time?

i. Yes.
ii. No.

7. If willing, please state the species of large invertebrate and vertebrate prey the primates in question have changed too as well as when this occurred.

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8. In which season does your sightings of large invertebrate and vertebrate exploitation occur most often?

i. Dry seasons
ii. Wet seasons
iii. The primate species that I research have no pattern when consuming large invertebrates and vertebrates. They consume them equally in both seasons opportunistically.

Part 3.

The next portion of this survey is applicable to current short-term studies that have

a research period of five years or less, in addition to a publication date after the year 2000.

1. During the course of your research did you notice:

i. No predation events by the primates that you research.
ii. Less than five predation events by the primates that you research.
iii. Five – ten predation events by the primates that you research.
iiii. Over ten predation events by the primates that you research.

2. If over ten predation events please specify the number

____

3. During which season did these predation events occur most frequently?

i. The predation events occurred in dry seasons.
ii. The predation events occurred in wet seasons.
iii. The predation events occurred in both wet and dry seasons.

4. Do the primate species that you study reside in a fragmented forest?

i. Yes
ii. No

5. Did you happen to notice if the hunters were primarily males or females?

i. The hunters were primarily males
ii. The hunters were primarily females
iii. There was no difference in the sex of the hunters because both hunted equally
iv. I did not notice the sex of the hunters

6. What mode of hunting did the primates use to capture their prey?

i. Opportunistic hunting
ii. Cooperative hunting

7. Did the primates share their meat?
i. Yes, meat sharing occurred
ii. Meat sharing did not occur

If you answered yes to question 7, please answer question 8.

8. Did the meat sharing occur only with kin members or did meat sharing occur with other individuals in the group?

i. Meat sharing only occurred with kin members (i.e infants)
ii. Meat sharing occurred with other troop members
iii. Meat sharing occurred with both kin members and other troop members

9. Did any juveniles hunt the large invertebrates and invertebrates?

i. Yes the juveniles exploited prey
ii. No the juveniles were not interested in exploiting any prey items

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Survey complete. Thank-you for your time and insight.

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Appendix 6. Survey Results *

Species studied by participant	Diet	No Predation 1970-2015	> 5 predation events 1970-2015	5-10 predation events 1970-2015	10 > predation events 1970-2015	Fragmented Forest	Seasonal preference for hunting meat	Sex difference in hunters	Hunting Strategy	Meat Sharing	Meat Sharing with kin or troop	Did juveniles hunt?
Gorillas (*Gorilla beringei*)	Fl	Yes	-	-	-	-	-	-	-	-	-	-
Olive baboons (*Papio anubis*)	O	-	-	Yes	-	No	Wet and Dry	No	OPP	Yes	Kin and troop members	Yes
Long-tailed macaque *(Macaca fascicularis)*	O	Yes	-	-	-	No	-	-	-	-	-	-
Ebony langur (*Trachypithecus auratus*)	Fl	-	Yes	-	-	No	Dry	No	OPP	No	-	-
Nepal gray langur (*Semnopithecus schistaceus)*	Fl	Yes	-	-	-	No	-	-	-	-	-	-
Phayre's leaf monkey (*Trachypithecus phayrei crepusculus)*	Fl	Yes	-	-	-	No	-	-	-	-	-	-
Bearded capuchins *(Sapajus libidinosus)*	O	-	-	Yes	-	Yes	Wet and Dry	No	OPP	Yes	Kin and troop members	Yes
White-faced capuchins *(Cebus capuchinus)*	O	-	-	-	Yes	Yes	Wet and Dry	No	OPP	No	Neither	Yes
Central American squirrel monkey (Saimiri oerstedii)	FR	Yes	-	-	-	Yes	-	-	-	-	-	-
Howler monkey (Alouatta palliate)	FR	Yes	-	-	-	-	-	-	-	-	-	-

** FL = Folivorous, O= Omnivorous, FR= Frugivorous, OPP= Opportunistic Hunting

Appendix 7. Conservation Status of Omni-frugivores **

Species	Status	IUCN Red List Database
Chimpanzees	Endangered	http://www.iucnredlist.org/details/15933/0
Bonobos	Endangeredg	http://www.iucnredlist.org/details/15932/0
Chacma baboons	Least Concern	http://www.iucnredlist.org/details/16022/0
Olive baboons	Least Concern	http://www.iucnredlist.org/details/40647/0
Yellow baboons	Least Concern	http://www.iucnredlist.org/details/16021/0
Diana Monkey	Vulnerable	http://www.iucnredlist.org/details/4215/0
L’Hoest Monkey	Vulnerable	http://www.iucnredlist.org/details/4220/0
Red-tailed monkey	Least Concern	http://www.iucnredlist.org/details/4212/0
Blue Monkey	Least Concern	http://www.iucnredlist.org/details/4221/0
Barbary Macaque	Endangered	http://www.iucnredlist.org/details/12561/0
Vervets	Least Concern	http://www.iucnredlist.org/details/136271/0
Patas Monkey	Least Concern	http://www.iucnredlist.org/details/8073/0
Lion-tail macaques	Endangered	http://www.iucnredlist.org/details/12559/0
Japanese macaques	Least Concern	http://www.iucnredlist.org/details/12552/0
Bonnet macaques	Least Concern	http://www.iucnredlist.org/details/12558/0
Northern Pig-tailed macaques	Vulnerable	http://www.iucnredlist.org/details/39792/0
Assamese macaque	Near Threatened	http://www.iucnredlist.org/details/12549/0
Long-tailed macaques	Least Concern	http://www.iucnredlist.org/details/12551/0
Black-crested macaques	Critically Endangered	http://www.iucnredlist.org/details/12556/0
Tonkean macaques	Vulnerable	http://www.iucnredlist.org/details/12563/0
Eastern black-crested gibbon	Critically Endangered	http://www.iucnredlist.org/details/41642/0
Western black-crested gibbon	Critically Endangered	http://www.iucnredlist.org/details/39775/0
Javan gibbon	Endangered	http://www.iucnredlist.org/details/10550/0
Bornean gibbon	Endangered	http://www.iucnredlist.org/details/10551/0
Eastern hoolock gibbon	Vulnerable	http://www.iucnredlist.org/details/39877/0
Sumatran orang-utans	Endangered	http://www.iucnredlist.org/details/39780/0
Bornean orang-utans	Endangered	http://www.iucnredlist.org/details/17975/0
White-faced capuchins	Least Concern	http://www.iucnredlist.org/details/43934/0
Ka’apor capuchins	Critically Endangered	http://www.iucnredlist.org/details/40019/0
Tufted capuchins	Near Threatened	http://www.iucnredlist.org/details/136717/0

Bearded capuchins	Least Concern	http://www.iucnredlist.org/details/136346/0
Amazonian squirrel monkey	Least Concern	http://www.iucnredlist.org/details/41537/0
Geoffroy spider monkey	Endangered	http://www.iucnredlist.org/details/2279/0
Black-faced spider monkey	Endangered	http://www.iucnredlist.org/details/41547/0
White-bellied spider monkey	Endangered	http://www.iucnredlist.org/details/2276/0
Black lion tamarins	Endangered	http://www.iucnredlist.org/details/11505/0
Mustached tamarins	Least Concern	http://www.iucnredlist.org/details/41526/0
Saddle-back tamarins	Least Concern	http://www.iucnredlist.org/details/39947/0
Common marmosets	Least Concern	http://www.iucnredlist.org/details/41518/0
Buffy-headed marmosets	Endangered	http://www.iucnredlist.org/details/3571/0
Woolly monkey	Vulnerable	http://www.iucnredlist.org/details/11175/0
Common brown lemurs	Near Threatened	http://www.iucnredlist.org/details/8207/0
Collared brown lemurs	Endangered	http://www.iucnredlist.org/details/8206/0
Red ruffed lemurs	Critically Endangered	http://www.iucnredlist.org/details/22920/0
Black lemurs	Vulnerable	http://www.iucnredlist.org/details/8212/0
Blue-eyed black lemurs	Critically Endangered	http://www.iucnredlist.org/details/8211/0
Ring-tailed lemurs	Endangered	http://www.iucnredlist.org/details/11496/0

** The conservation status of my sampled species as categorized by the IUCN Red List. Here are the definitions of the categories provided by the IUCN Red List (http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf).

1. **Least Concern**: the populations are at healthy levels (IUCN Red List: categories and critieria. http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf).

2. **Vulnerable**: “An observed, estimated, inferred or suspected population size reduction of ≥50% over the last 10 years or three generations, whichever is the longer, where the causes of the reduction are clearly reversible AND understood AND ceased.” (IUCN Red List: categories and critieria, pp. 20. http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf).

3. **Endangered**: “An observed, estimated, inferred or suspected population size reduction of ≥70% over the last 10 years or three generations, whichever is the longer, where the causes of the reduction are clearly reversible AND understood AND ceased.” (IUCN Red List: categories and critieria, pp. 17. http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf).

4. **Critically Endangered**: “An observed, estimated, inferred or suspected population size reduction of ≥90% over the last 10 years or three generations, whichever is the longer, where the causes of the reduction are clearly reversible AND understood AND ceased.” (IUCN Red List: categories and critieria, pp. 16. http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf).