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The Effect of Food Provisioning on the
Nutrient Intake of Wild and Captive
Primates - Implications for the
Conservation Management of Wild and
Captive Populations

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Abstract

Many non-human primate populations worldwide are threatened with extinction. Various measures are taken to save these species. Amongst these efforts are habitat protection, restoration, and public education, including wildlife tourism. To efficiently protect and restore wildlife habitats, ecological knowledge, such as the nutritional ecology of target species, is essential. Information on the foraging behaviour and nutritional requirements of a species will be useful for the protection and restoration of foods that are important components of a species' diet. Furthermore, knowledge on animal nutritional ecology is required in circumstances where animals are fed by humans, as can occur in wildlife tourism settings. With such information, efforts can be made to provide diets which are nutritionally balanced, reducing the likelihood of negatively impacting the health and welfare of target animals. This study was undertaken to investigate food and nutrient intake under three levels of human dietary interference using primates as models: no interference, partial provisioning, and full provisioning.

A wild golden snub-nosed monkey (*Rhinopithecus roxellana*) troop was investigated to determine their food and nutrient intake in a natural setting. A positive correlation between food availability and food choice was not found. On the nutrient level, the troop's proportional consumption of crude protein, lipids, and non-structural carbohydrates varied with the seasonal availability of these nutrients while the consumption of neutral detergent fibre increased

relative to its availability and that of lignin decreased. Differences in the foraging behaviour between different seasons and between monkeys of different age, sex, or reproductive status were not detected. However, age and sex based differences in proportional nutrient intake patterns were found. Juveniles had a greater proportional intake of all nutrients than adults (per kg of metabolic body mass) and females had a greater proportional intake of nearly all nutrients than males (per kg of metabolic body mass).

To investigate the effects of food provisioning at a wildlife tourism centre in China, the proportional nutrient intake of a semi-wild golden snub-nosed monkey troop was determined and compared with that of the wild troop. The provisioned troop's foods had a greater proportional contribution of non-structural carbohydrates and lipids and a smaller proportional contribution of neutral detergent fibre and lignin than foods consumed by the wild troop. The proportional nutrient intake of the provisioned troop, compared with that of the wild troop, was greater in non-structural carbohydrates and lower in crude protein, neutral detergent fibre, and lignin. Proportional lipid intake by the provisioned troop was lower than the wild troop in summer but greater in autumn.

To investigate the nutritional ecology of a completely captive, and hence nutritionally dependent, troop of primates, the Auckland Zoo's black-handed spider monkey (*Ateles*

geoffroyi) troop was studied. The group's daily macronutrient intake pattern was investigated as was the daily food and nutrient intake of monkeys based on age, sex, and social rank. The troop maintained a relatively stable non-protein energy to protein energy ratio intake across multiple days suggesting they were not facing dietary constraints. Juveniles had a greater daily food and nutrient intake (per kg of metabolic body mass) than adults and a greater intake of food and all nutrients except for non-structural carbohydrates than geriatric monkeys. Daily food and nutrient intake differences between monkeys based on sex and social rank were not detected.

The findings of this study advance our understanding of the effect of human provisioning on the foraging and nutrient intake patterns of wildlife populations. This information can be used in the development of habitat protection and restoration plans for golden snub-nosed monkeys to ensure that important foods remain available in their habitat. Furthermore, findings on the potential impacts of an unnatural diet on the nutrient intake of provisioned animals can be used to improve the conservation management of primate populations used for wildlife tourism.

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Chapter 1: Introduction

Non-human primate populations, which include prosimians, monkeys, and apes, are declining worldwide (Schwitzer et al. 2014). Over half of known primate species and subspecies are threatened with extinction (Estrada et al. 2017; IUCN 2012). The threats faced by primates include trade (Eudey 2008; Nijman et al. 2011), habitat loss (Chapman & Gogarten 2012), hunting for bushmeat (Linder & Oates 2011; Milner-Gulland & Bennett 2003; OATES 1996), climate change (Dunbar 1998), and disease (Bermejo et al. 2006). These circumstances call for the management and conservation of these animals and their habitats. Effective management requires knowledge on the habitat requirements of target populations, as well as the effectiveness of management strategies.

1.1 Conservation and Management of Endangered Species

There are various strategies used by wildlife managers and conservationists to assist in population recovery and ecosystem restoration. Habitat restoration (Fellowes et al. 2008; Miller & Hobbs 2007) or protection (Laidlaw 1998) can be used to help species, and even ecosystems, that are threatened (Dobson et al. 1997; Kleiman 1989). These processes involve planting native plants to restore and expand usable habitat, such as occurred in the habitat of the critically endangered Hainan gibbon (*Nomascus hainanus*) (Fellowes et al. 2008), and establish biological conservation areas that vary in the types and levels of permissible activities (e.g.

Dudley 2008). Habitat restoration or protection projects are not always successful, however (Browne & Hecnar 2007; Smokorowski et al. 1998), illustrating the complexities of ecological conservation. Despite variation in success, habitat restoration and protection are valuable tools that can be used in efforts to conserve primates. For effective habitat management, information on the nutritional requirements of primates and key resources in their habitat that sustain their nutritional needs is important.

Another strategy of conservation is raising public awareness through wildlife tourism (Higginbottom 2004). Wildlife tourism can involve the management of semi-captive animals in at least somewhat natural settings or may involve the management of fully captive animals in facilities such as zoos (Higginbottom 2004). Non-captive and captive forms of tourism often differ in their contribution to conservation. Some zoos have been involved with breeding and releasing animals into the wild (Kleiman 1989; Kleiman et al. 1986). Zoos can also assist in animal conservation by managing the genetics of captive populations (Higginbottom 2004) and can also exchange valuable information, such as data on behaviour and reproduction, with scientists who work with the species in the wild (Ryder & Feistner 1995). Zoos often make financial contributions to conservation efforts and/or encourage visitors to make such contributions while also raising public awareness and interest in wildlife. Some non-captive tourism operations offer the same benefits to conservation (Higginbottom 2004). For example, wildlife tourism in Shennongjia National Nature Reserve (China) led to increased financial

support for the conservation of a flagship species and has raised public awareness of the species' population status (Xiang et al. 2011). While variation exists in the extent to which tourism contributes to species conservation, it is clear that conservation efforts can benefit from well operated tourism.

Despite these potentials, there are also limitations and potential disadvantages to tourism that need to be considered. There are environmental concerns such as habitat modification and pollution which can occur through the clearing of areas, loss of native plants, the introduction of exotic species, and the use of chemicals (Reynolds & Braithwaite 2001). Such modifications are likely to occur during the preparation of and running of wildlife tourism operations. There can also be direct impacts on the target animals due to confinement and being under human care. These impacts include stress and increased aggression (Berman et al. 2007; McCarthy et al. 2009), behavioural changes such as stereotyped behaviour and habituation (Reynolds & Braithwaite 2001), and nutritional changes if consuming an unnatural diet (Reynolds & Braithwaite 2001). Such possible negative impacts, which can occur at tourism facilities ranging from zoos and sanctuaries to operations in the wild, need to be considered and research should be undertaken to determine the impact of various practices on focal animals. For example, health complications such as obesity, dental damage, and gastrointestinal problems can arise when animals do not have access to a diet that provides balanced nutrition (Johnson-Delaney 2008; Plowman 2013; Schwitzer & Kaumanns 2001).

1.2 Food and Nutrient Intake

Wildlife management and conservation often deal with habitat destruction or alteration. Previous studies on how species respond to such changes found variable results. Habitat loss due to conversion of forests to agricultural lands is the greatest threat to primates (Estrada et al. 2017). A large number of primate taxa are capable of utilizing such areas to some degree, however (Estrada et al. 2012). Some primates, for example, take advantage of cultivated lands by consuming crops (Estrada et al. 2012; McLennan 2013; Naughton-Treves et al. 1998; Riley et al. 2013; Saj et al. 1999). If and how the integration of cultivated foods into their diet affects their nutrient intake and ultimately their fitness has not been extensively researched, however. One such study found weight gain in olive baboons who integrated crops into their diet (Forthman-Quick & Demment 1988), demonstrating a likely outcome of a notable dietary shift. Despite the fact that some primates have been able to adapt to various degrees of habitat loss, the general outcome has been population decline (Estrada et al. 2017). The effects of habitat loss thus need to be considered in studies on primate conservation, including foraging and nutritional studies.

Furthermore, conventional foods, which are not natural components of animals' diets, are introduced to animals as food provisioning is a technique used for tourism purposes (Dubois & Fraser 2013; Green & Higginbottom 2001; Hines 2011; Murray et al. 2016; Newsome & Rodger 2013; Orams 2002; Schwitzer & Kaumanns 2001). Animals kept in captivity are also

sustained on foods that do not naturally occur in their natural habitats. This could have an effect on the ability of such animals to obtain a balanced diet and may have adverse impacts on their overall fitness (Murray et al. 2016; O'Leary 1996). For example, the consumption of large amounts of human derived foods have led to weight gain in Barbary macaques (*Macaca Sylvanus*) (O'Leary 1996) and olive baboons (*Papio Anubis*) (Forthman-Quick & Demment 1988). Similarly, obesity has been noted in captive primates such as ruffed lemurs (*Varecia variegata*) (Schwitzer & Kaumanns 2001).

It is thus necessary to study animal food and nutrient requirements or, in the absence of controlled conditions, food and nutrient intake patterns. Although determining the precise nutritional requirements of wild animals may not be possible due to constraints involved with observing animals in the wild, such studies will still allow us to gain a better understanding of their food and nutrient intake. This will lead to habitats being managed in such a way that allows animals to have continued access to foods that are important components of their diet. Additionally, diets offered to provisioned or captive wildlife can be prepared using data from such studies as a guideline, hopefully reducing the likelihood of providing diets that adversely affect the health of target animals.

1.2.1 Foraging Behaviour

Nutritional intake involves the acquisition, manipulation, and ultimately consumption of foods. Both foraging behaviour and nutritional intake are thus relevant to studies on animal

nutritional ecology, the field of study concerned with how animals interact with their environment at the nutritional level (Raubenheimer et al. 2009). Studies on primate foraging behaviour are extensive and cover a wide variety of taxa. Primate food consumption has been related to various factors such as food availability (Hanya et al. 2003; Heiduck 1997; Remis 2003; Simmen & Sabatier 1996), the physical characteristics of foods (e.g. size, hardness) (Dew 2005; Guillotin et al. 1994; Kinzey & Norconk 1990), behavioural strategies (Tsuji et al. 2013), and the consumer's anatomical/physiological characteristics (Chivers & Hladik 1980; Remis 2003). Furthermore, many studies document what foods and food types (leaves, fruit, bark, etc.) are consumed by animals. These patterns are sometimes related to factors such as spatial or temporal changes (Garber 1993; McConkey et al. 2003; Tsuji et al. 2013; Zhou et al. 2006). For example, a Francois' langurs (*Trachypithecus francoisi*) troop's diet mainly consisted of young leaves from April Through September and then changed to being mainly consisted of stems, petioles, and seeds from October to March (Zhou et al. 2006).

Previous studies relating food consumption to various nutritional aspects of foods have also been conducted on primates (Behie & Pavelka 2012; Dew 2005; Marks et al. 1988; Oates et al. 1980; Remis 2003; Simmen & Sabatier 1996). Two types of leaf monkeys, the banded leaf monkey (*Presbytis melalophos*) and the red leaf monkey (*Presbytis rubicunda*), demonstrated preference for leaves that were low in fibre and high in protein and fruits and seeds there were high in storage carbohydrates and fat yet low in sugars (Davies et al. 1988).

Additionally, studies relating primate biomass to plant nutritional profiles can be found in the literature. For example, Colobine biomass was positively correlated with the nitrogen to fibre ratio of plants in parts of Malaysia (Waterman et al. 1988).

1.2.2 Hypotheses Explaining the Nutritional Influences on Animal Food Choice

Various hypotheses explaining animal food selection have been proposed and tested. Five main hypotheses have been applied to primate dietary studies (Felton et al. 2009a): energy maximization, nitrogen maximization, secondary plant metabolite avoidance/regulation, dietary fibre limitation, and nutrient balancing.

The first four hypotheses suggest that through food selection, animals seek to maximize the consumption of certain factors (e.g. energy or nitrogen) or to avoid certain factors (e.g. fibre, secondary metabolites). Support for these hypotheses have been mixed with some studies being in alignment (e.g. energy maximization: Belovsky 1978; Laska et al. 2000; nitrogen maximization: McKey et al. 1981; Mowry et al. 1996) while other studies have not (e.g. energy maximization: Basey & Jenkins 1995; Bergman et al. 2001; secondary metabolite avoidance: Fashing et al. 2007; nitrogen maximization: Hewson-Hughes et al. 2013; Rothman et al. 2011b). The nutrient balancing hypothesis is unique in that it considers the interactions between multiple nutrients and any grouping of nutrients/factors (e.g. macronutrients, micronutrients, energy) can be included. This hypothesis proposes that animals aim to intake a specific balance of nutrients (Raubenheimer & Simpson 1997). It has successfully explained animal nutrient

intake in both laboratory and field studies and across multiple taxa (e.g. Felton et al. 2009b; Gosby et al. 2013; Hewson-Hughes et al. 2013; Hewson-Hughes et al. 2011; Johnson et al. 2013; Lee et al. 2008; Raubenheimer & Jones 2006; Rothman et al. 2008b; Simpson & Raubenheimer 1995).

1.2.3 Nutritional Balancing

Studies using the nutritional balancing model demonstrate that animals aim to ingest an optimal nutrient ratio, their nutrient target (Simpson & Raubenheimer 1995). The position of this target (i.e. the specific nutrient ratio) has been determined experimentally for various species such as German cockroaches (*Blattella germanica*) (Jones & Raubenheimer 2001), domestic cats (*Felis catus*) (Hewson-Hughes et al. 2011), and domestic dogs (*Canis lupus familiaris*) (Hewson-Hughes et al. 2013). Observations on the nutrient intake of wild animals can also demonstrate nutrient targets, as was seen in a study on a female chacma baboon (*Papio hamadryas usinus*) (Johnson et al. 2013). The baboon maintained a daily non-protein energy to protein energy ratio of 5:1 kcal for 30 days despite this ratio not being found in her foods (Johnson et al. 2013). It is this maintenance of a relatively consistent nutrient ratio that suggests a nutritional target is being met.

When available foods are not balanced (i.e. do not contain the animal's ideal nutrient ratio), there can be various outcomes. If there are foods that are imbalanced but complimentary, and hence lie on both sides of the target ratio, an animal can ultimately arrive at their nutritional

target by selectively consuming food items with a complimentary nutrient composition (Raubenheimer & Simpson 1997). If, however, circumstances are such that available foods are imbalanced and not complimentary (Raubenheimer & Simpson 1997), compromises need to be made. Such compromises include nutrient prioritization where the intake of one nutrient is maintained at relatively constant levels while the intake of other nutrients is allowed to fluctuate. In the wild, nutrient prioritization can be detected during times of nutritional constraint due to changes in food availability. For example, Peruvian spider monkeys (*Ateles chamek*) prioritised protein energy when unable to meet the macronutrient balance reached when balanced and unbalanced, yet complimentary, foods were available (Felton et al. 2009b). Mountain gorillas (*Gorilla beringei*), on the other hand, prioritized non-protein energy when they were unable to reach their balanced macronutrient ratio using available foods (Rothman et al. 2011b). Similar to spider monkeys, humans (*Homo sapiens sapiens*) demonstrate protein prioritization when faced with nutritional constraints (Gosby et al. 2013). Plotting daily nutrient intake points in nutritional space and analysing the patterns thus suggest whether an animal is reaching his/her nutrient target (maintenance of a consistent ratio across days) or is constrained (a vertical or horizontal pattern due to the prioritization of a nutrient).

Although it is possible to collect robust data sets in field studies, it should be noted that studies in the wild may be constrained by challenging conditions (e.g. visibility constraints, difficulties in making full day observations) and the inability to experimentally confirm initial

findings through controlled feeding trials. The investigation of nutrient intake patterns using multivariate analyses (i.e. analyses incorporating more than one nutrient/factor) such as the geometric framework (Simpson & Raubenheimer 1995) is still possible despite these challenges, however. Data on animal food and nutrient intake trends, even in the absence of nutritional goal determination, can benefit conservation efforts both with wild and provisioned animals through strengthening our understanding of their nutritional ecology.

As the need to resort to nutrient prioritisation occurs when animals are unable to reach a nutrient goal, nutritional compromise may occur in situations involving captivity or supplemental feeding if animals are not provided with a balanced diet. Despite this and despite the popularity of both captive animal populations and wildlife tourism, which sometimes uses supplemental feeding, this area of nutrition has not been researched in depth. The aim of this study is to assess whether wildlife provisioning affects the ability of animals to obtain a balanced nutritional intake. This will be accomplished through investigating food and nutrient intake of primates under the following three levels of human dietary interference: no interference, food provisioning in a semi-captive population, and full food provisioning in a fully captive situation. Golden snub-nosed monkeys (*R. roxellana*) were used as a model for the first two levels of human interference. In the absence of a captive golden snub-nosed monkey troop, a captive black-handed spider monkey (*A. geoffroyi*) group was used as a model to investigate food and nutrient intake in fully provisioned primates. The information obtained

from this study will strengthen our understanding of wild golden snub-nosed monkey food and nutrient intake and will help improve the design of supplementary diets for both species, hopefully reducing the likelihood of target animals succumbing to health risks associated with imbalanced nutritional intake.

1.3 Study Species

1.3.1 Golden Snub-Nosed Monkeys (*Rhinopithecus roxellana*)

1.3.1.1 Taxonomy, Distribution, and Abundance

Golden snub-nosed monkeys are members of the Colobine subfamily in the Cercopithecidae primate family. They are one of five snub-nosed monkey species in the genus *Rhinopithecus*. The other four species are the black snub-nosed monkey (*Rhinopithecus bieti*), the gray snub-nosed monkey (*Rhinopithecus brelichi*), the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*), and the Burmese snub-nosed monkey (*Rhinopithecus strykeri*) (Roos et al. 2013). *R. strykeri* is found in Burma and China, *R. avunculus* is found in Vietnam, and the remaining species are endemic to China (Roos et al. 2013).

Golden snub-nosed monkeys occupy broadleaf, conifer, and mixed broadleaf/conifer forests in China's Qionglai, Minshan, Daba, and Qinling Mountains (Renmei et al. 1998) and occurs in the following provinces: Hubei, Shaanxi, Sichuan, Gansu (Groves 2001). This species occupies areas ranging from 1,500 to 3,300 m above sea level (Hu 1998) and lives in highly seasonal areas (Guo et al. 2007).

R. roxellana has been divided into three subspecies (Yingxiang et al. 1998). *Rhinopithecus roxellana hubeiensis* is found in western Hubei and southeastern Sichuan and is characterised by paler fur, fused premaxillae, and absent or reduced nasal bones. *Rhinopithecus roxellana roxellana* occurs in southern Gansu and western Sichuan and are characterised by having a dull-golden coat and dusky blackish-brown limbs. *Rhinopithecus roxellana qinlingensis*, the focal species of this study, inhabit the Qinling Mountains in Shaanxi province and have coats that are more brilliantly coloured and have a narrower braincase.

Genetic studies have found evidence of bottlenecks in some snub-nosed monkey populations. A study which analysed samples from three regions (Qinling Mountains, Sichuan, and Shennongjia) suggests that there was a bottleneck within the past 15,000 years (Li et al. 2003). Other studies have focused on more specific areas. For example, the population in Shennongjia Nature Reserve was specifically studied and the results suggests a 37-fold decrease in the population sometime in the past 500 years (Chang et al. 2012). A study which focused on populations in the Qinling Mountains, however, found no evidence of any bottlenecks (Huang et al. 2016) although an earlier study suggested a bottleneck in the Qinling mountain (and Sichuan) populations (Pan et al. 2005). The inconsistency in these results is potentially due to the small sample size used by Pan *et al.* (Huang et al. 2016). In terms of population size, there are an estimated 12,750 golden snub-nosed monkeys remaining in the

wild (Yingxiang et al. 1998; Yongcheng 2008). According to the IUCN, their population is decreasing and the species is endangered (Yongcheng 2008).

1.3.1.2 Previous Studies on Snub-nosed Monkey Diet

Golden snub-nosed monkeys are foregut fermenters (National Research Council 2003). Colobine monkeys in general are noted for their gastrointestinal specializations which include expanded foreguts which house fermenting bacteria (National Research Council 2003). Monkeys in the *Rhinopithecus* genus are referred to as quadripartite, as opposed to tripartite (Caton 1998), as they have a presaccus which stores ingesta prior to the active site of bacterial fermentation, the saccus (Kay et al. 1976; Nijboer & Clauss 2006). The colon is also suspected to be an important site of fermentation based on a study on two king colobus monkeys (*Colobus polykomos*) (Kay et al. 1976). A study on two tripartite Colobines, the Hanuman langur (*Presbytis entellus*) and the silvered leaf monkey (*Presbytis cristatus*), suggests that the products of microbial fermentation make significant contributions to these monkeys' nutritional intake (Bauchop & Martucci 1968).

Golden snub-nosed monkeys consume leaves and other plant parts such as fruit, seeds, and bark (Guo et al. 2007; Li 2006; Li et al. 2010). Some populations consume lichens (Guo et al. 2007; Li 2006; Liu et al. 2013) while other do not (Li et al. 2010). Although rare, animals such as birds and invertebrates have also been recorded in their diet (Li et al. 2002; Zhao 2008, pers. obs.). Previous studies have documented the consumption of 100 different plant species

by *R. roxellana* in three areas: Shennongjia Nature Reserve (SNR), Zhouzhi National Nature Reserve (ZNNR), and Qingmichuan Nature Reserve (QNR) (Guo et al. 2007; Li 2006; Li et al. 2010; Li et al. 2002; Liu et al. 2013).

Some dietary differences were found between different populations in terms of food species (Guo et al. 2007; Li 2006; Li et al. 2010; Li et al. 2002; Liu et al. 2013) and seasonal variations (Guo et al. 2007; Li et al. 2010). This species consumes leaves and fruit in summer in SNR, ZNNR, and QNR (Guo et al. 2007; Li 2006; Li et al. 2010; Liu et al. 2013). Lichen consumption was also observed during summer months in SNR (Li 2006; Liu et al. 2013). Autumn seed and lichen consumption was observed in all three areas (Guo et al. 2007; Li 2006; Li et al. 2010; Liu et al. 2013) while fruit was also consumed in SNR during autumn (Li 2006; Liu et al. 2013). During winter, lichen and seeds made up most of the diet of the monkeys in ZNNR (Guo et al. 2007), leaves, buds and bark were consumed in QNR (Li et al. 2010), and lichen consumption was noted in two studies in SNR (Liu et al. 2013; Li 2006) while one of the studies in SNR also found seed and bud consumption (Liu et al. 2013). Leaves and lichen make up most of the spring diet in SNR (Liu et al. 2013; Li 2006) while bud consumption was also noted in one study in this area (Liu et al. 2013). Lichen and bark were the main contributors to the diet of monkeys in ZNNR (Guo et al. 2007). These studies show that while there is dietary overlap between areas in terms of food types consumed, there are also differences. Another possibility is that there are not as many differences as these studies suggest and that

disparities in observations could be the result of methodologies and/or variation in constraints (e.g. visibility) across sites.

Studies of golden snub-nosed monkey diet at the nutrient level are limited in the literature. One published study on a troop in Shennongjia National Nature Reserve found that their foods are lower in fibre content than non-food items while the protein to fibre ratio of foods and non-foods did not differ (Liu et al. 2013). These monkeys consumed leaves that were higher in water soluble carbohydrate content than non-food leaves while foods and non-foods did not differ in protein content (Liu et al. 2013). Studies on the nutrient content of foods consumed by populations in other areas are lacking.

There is a wild golden snub-nosed monkey population in the Qinling Mountains that has been studied for many years and is thus habituated to humans. This allows for close observations to be made on these animals. This species' charisma has also resulted in it being popular in wildlife tourism sites in China. There are thus groups of monkeys subjected to food provisioning. The accessibility of a habituated wild population and a provisioned troop make this species appropriate for investigations into food and nutrient intake in primates under two levels of human dietary interference: no interference and partial interference through provisioning in a semi-captive situation.

1.3.2 Black Handed Spider Monkeys (*Ateles geoffroyi*)

1.3.2.1 Taxonomy, Distribution, and Abundance

Spider monkeys are New World monkeys in the Atelidae family. There are seven recognized spider monkey species: the white-bellied spider monkey (*A. belzebuth*), the Peruvian spider monkey (*A. chamek*), the black-headed spider monkey (*A. fusciceps*), the brown spider monkey (*A. hybridus*), the white-cheeked spider monkey (*A. marginatus*), the red-faced spider monkey (*A. paniscus*), and, the focal species of this study, the black-handed spider monkey (*A. geoffroyi*). *A. geoffroyi* consists of seven sub-species (Rylands et al. 2006). It should be noted, however, that the taxonomy of this species at the subspecies level is not well understood and a revision has been recommended (Rylands et al. 2006).

Most spider monkeys are found exclusively in South America (IUCN 2010). The two exceptions are a *A. fusciceps*, whose northern range extends into Panama, and *A. geoffroyi* which is found in North America (Mexico), Central America (Costa Rica, Nicaragua, Panama, El Salvador, Honduras, Guatemala, Belize), and the northern tip of South America (Columbia) (Cuarón et al. 2008; Rylands et al. 2006). Throughout its range, *A. geoffroyi* inhabits tropical forests (wet, moist, and dry), deciduous forests, semi-evergreen forests, and coastal regions (Di Fiore & Campbell 2007; Gonzalez-Zamora et al. 2009; Ramos-Fernández & Ayala-Orozco 2003).

A. geoffroyi is classified as endangered (Cuarón et al. 2008). All other species of spider monkey, with the exception of *A. paniscus* which is classified as vulnerable (Mittermeier 2008b), are either endangered or critically endangered (Boubli 2008; Cuarón 2008; Mittermeier 2008a; Urbani 2008; Wallace 2008). All spider monkey species are reported as decreasing by the IUCN (Boubli 2008; Cuarón 2008; Mittermeier 2008a, b; Urbani 2008; Wallace 2008). Reports on the abundance of the black-handed spider monkey are rare with estimates only being available for 3 of 7 subspecies (Freese 1976; Méndez-Carvajal 2013; Ramos-Fernández & Ayala-Orozco 2003).

1.3.2.2 Previous Studies on Spider Monkey Diet

The diet of *A. geoffroyi* is mainly composed of fruit, leaves, flowers, seeds, and small amounts of invertebrates (Cant 1990; Chaves et al. 2011; Di Fiore & Campbell 2007; Gonzalez-Zamora et al. 2009) with fruit making up majority of their diet followed by leaves (González-Zamora et al. 2009). Wild spider monkeys consume many different plant species but those from the families *Moraceae* and *Fabaceae* are favoured (González-Zamora et al. 2009). The diet of this species is affected by habitat quality with those inhabiting fragments, as opposed to areas of continuous forest, altering their diet to include more leaves and plants that are more available than typical dietary items (Chaves et al. 2012). Both seasonal and spatial variation in diet (in terms of species consumed) occur in this species, likely due to differences in food

availability (Gonzalez-Zamora et al. 2009). It is unknown, however, if such differences in food choice also reflect differences in nutrient requirements.

The food and nutrient intake of an *A. chamek* troop in Bolivia has been studied. The nutrient composition of their foods has also been determined. These monkeys aimed for a non-protein energy to protein energy ratio of 8:1 (Felton et al. 2009b). When constraints prevented them from reaching this goal, they prioritised their daily protein energy intake (Felton et al. 2009b). The monkeys had three different nutrient intake patterns based on resource availability. When ripe figs, their main foods which are nutritionally balanced, were abundant, they mainly fed on these fruits (Felton et al. 2009c). When ripe figs and other fruits were less abundant, the monkeys ate a mixture of foods that were nutritionally complementary. During times of fig shortage, the monkeys over consumed non-protein energy which is proposed to be a method of accumulating and storing excess fat for times of food shortages (Felton et al. 2009b). Whether these nutrient intake trends are representative of other populations of this species or of spider monkeys in general remains to be determined.

Black-handed spider monkeys, being very charismatic and hence popular, are commonly kept in zoos with more than 500 individuals registered in Zoological Information Management Systems (ZIMS) (ISIS - ZIMS 2.3). Their popularity and abundance in captivity make them an ideal species for studies on the effects of full dietary provisioning. Within New Zealand, spider monkeys can be found at 4 zoological institutions: Auckland Zoo, Hamilton

Zoo, Wellington Zoo, and Orana Wildlife Park. At the time of this study the Auckland Zoo troop, the focal troop, consisted of 16 individuals, varying in sex and age. Information on the diets offered to spider monkeys held at various institutions is not readily available, however. Understanding the nutritional requirements of captive animals is a necessity, particularly for a species as abundant in zoological institutions as the black-handed spider monkey. Such an understanding is required to ensure they are provided with an appropriate diet which has direct implications for their welfare.

1.4 Study Objectives and Thesis Design

The objectives of this thesis are:

1. To investigate food and nutritional intake in a wild golden snub-nosed (*R. roxellana*) monkey troop to understand these aspects of a troop foraging under natural circumstances and to determine whether food choice correlates with food availability in this troop. Furthermore, I investigated the effect of sex, age, and reproductive status on food and nutritional intake. I predict food choice in these monkeys would not reflect food availability as their food choice is expected to be influenced by nutritional requirements and not be solely based upon what is readily available. Differences in food and nutrient intake between different subsets of the troop are expected due to differences in the energetic demands of individuals based on age, sex, and reproductive status.

2. To investigate food and nutritional intake in a semi-captive, provisioned golden snub-nosed monkey troop to determine if and how provisioning alters the dietary intake of partially provisioned monkeys. As commercial fruits contain more sugar and less protein and fibre than wild foods (Schwitzer et al. 2009), I predict differences to be found between the nutrient intake patterns of provisioned monkeys and wild monkeys due to the use of commercial fruits at the wildlife tourism site.

3. To determine whether there are differences in food and nutrient intake between two seasons, summer and autumn, in both the wild and provisioned troop. Data collection was restricted to these two seasons due to logistical constraints (e.g. other students study the wild troop over winter, time restrictions). I predict seasonal changes in both food and nutrient consumption in the wild troop due to phenological changes in their habitat and anticipated changes in the monkeys' nutritional requirements across the seasons. Such changes were not expected to be found in the provisioned troop as the major part of their diet, the part offered by humans, was relatively stable across the two seasons. As this troop's diet was nutritionally restrictive, seasonal changes in their nutrient intake are not expected.

4. To determine food and nutrient intake in a captive black-handed spider monkey troop that is completely dependent upon humans for food and to assess whether the offered diet was balanced and allowed the monkeys to reach and maintain nutritional goals. I predict that the troop could reach and maintain a balanced diet as the offered diet was highly variable in

nutritional content. Such a diverse diet is expected to allow the monkeys to make dietary choices free of restrictions.

5. To determine daily food and nutrient intake based on the monkeys' age class, sex, and social rank. I predict there to be differences between adults and juveniles and males and females due to differences in energetic requirements. I also expect to find differences between monkeys differing in social rank due to factors such as competition and/or food monopolization by dominant individuals.

The thesis will consist of five chapters. Chapter One, "General introduction", provides background information, the rationale of this research, and the aims, objectives, and structure of the thesis.

Chapter two, "Food and Nutrient Intake in a Wild Golden Snub-nosed Monkey Troop", addresses objectives 1 and 3. This chapter focuses on food and nutrient intake in a wild golden snub-nosed monkey troop to understand what plant species and parts of plants are important foods during summer and autumn and whether food choice reflects food availability. Furthermore, food and nutrient intake based on age, sex, and reproductive status is determined.

Chapter three, "The Impacts of Food Provisioning on Nutrient Intake in the Golden Snub-nosed Monkey (*R. roxellana*)", addresses objectives 2 and 3. This chapter compares food and nutrient intake in wild golden snub-nosed monkeys with that of a troop at a wildlife tourism park which

had limited access to natural foods and was heavily provisioned. The knowledge obtained from this study has implications for the management of provisioned monkeys for tourism.

Chapter Four, “Nutritional Ecology in a Captive Environment: The Effect of Age, Sex, and Social Status on Black-handed Spider Monkey (*A. Geoffroyi*) Food and Nutrient Intake”, addresses objectives 4 and 5. This chapter investigates a troop of black-handed spider monkeys in a zoo and hence fully dependent on provisioned foods. I determined the range of macronutrient ratios (nutrient space) made available to these monkeys. Furthermore, through analysis of their daily macronutrient ratio intake pattern, I evaluated whether provided foods allow them to meet their nutritional goal or cause the monkeys to make nutritional compromises. I also investigated the effect of age, sex, and social status on food and nutrient intake patterns.

Chapter Five, “General discussion and conclusion”, provides an overview of the findings of this thesis, their implications to conservation and management, and discussions on the limitations of this study and suggestions for further research.

The findings from these studies will not only enrich our knowledge of primate nutritional ecology, but are also important for the habitat management of these species in the wild and management of populations subject to tourism or captivity.

Chapter 2: Food and Nutrient Intake in a Wild Golden Snub-nosed Monkey (*Rhinopithecus roxellana*) Troop



Adult male golden snub-nosed monkey in Zhouzhi National Nature Reserve. Photo by Brigitte Kreigenhofer.

2.1 Abstract

How animal food and nutrient intake are influenced by food availability, nutritional requirements, and an animal's age, sex, and reproductive status are ecological questions, exploring how animals interact with their environment under different circumstances. Such knowledge has implications for the population and habitat management of endangered species.

I investigated seasonal food choice and nutrient consumption in golden snub-nosed monkeys (*Rhinopithecus roxellana*) and investigated how such patterns compare with food and nutrient availability in their habitat. Additionally, if and how food and nutrient intake vary between subsets of the troop (based on age, sex, and female reproductive status) was investigated. A positive correlation between this troop's food intake food availability was not detected. Plant species and food type consumption did not vary between summer and autumn. The troop's proportional consumption of crude protein, lipids, and non-structural carbohydrates varied with the seasonal availability of these nutrients while the consumption of neutral detergent fibre increased relative to its availability and that of lignin decreased. While plant species and food type consumption did not vary based on age, sex, or reproductive status, differences were detected at the nutrient level. Juveniles consumed significantly greater proportions of crude protein, lipids, non-structural carbohydrates, neutral detergent fibre, and lignin than adults per kg of metabolic body mass. Statistically significant differences were also detected between adult females and adult males, with females consuming greater proportions of most nutrients per kg of metabolic body mass during both seasons. No differences were detected between

lactating and non-lactating females. These findings provide information on the food and nutrient intake of an endangered Colobine primate and further our understanding of the effects of food availability, age, sex, and physiological status on food and nutrient consumption

2.2 Introduction

From a wide range of food resources available in the environment, animals tend to selectively consume food items in order to achieve a balanced nutrient intake (Felton et al. 2009c; Johnson et al. 2013; Rothman et al. 2011b). However, this ability can be challenged by habitat loss and modification which may result in the loss of or reduction in biodiversity and hence important food items. This could impact animals' nutrient intake by altering the array of foods, and hence nutrients, that are available. Nutritional intake impacts animal fitness and survival. For example, drosophila longevity and fecundity were directly related to specific nutrient balances (Lee et al. 2008). Furthermore, relatively recent shifts in nutrient balance in the human diet is suspected to be involved with the obesity epidemic in our species (Raubenheimer et al. 2015). Animal foraging behaviour and nutritional intake are thus important aspects of animal ecology and are relevant to conservation efforts.

Animal foraging behaviour has been extensively studied. Such studies document the variety of foods consumed by animals and also reveal the variability in dietary diversity that occurs across species. For example, the diet of panda bears (*Ailuropoda melanoleuca*) inhabiting the Qinling Mountains is mainly composed of only two bamboo species, the wood

bamboo (*Bashania fargesii*) and the arrow bamboo (*Fargesia qinlingensis*) (Nie et al. 2015). Other species are much less specialized in their diet. Black spider monkeys (*Ateles paniscus*), red howler monkeys (*Alouatta seniculus*), and tufted capuchins (*Cebus apella*) in French Guiana, for example, consume 133 different plant species (Simmen & Sabatier 1996). Although many different plants were consumed, preferences were noted. One plant family, *Sapotaceae*, dominated the diets of all 3 monkeys (Simmen & Sabatier 1996). Such studies demonstrate the dietary range of different species, illustrating the plant species that are important to their diets. Such data are important for the development of conservation management plans so that key dietary species can be protected.

For plant consumers, plant phenological changes heavily influence food type availability (e.g. leaves, fruit, pollen). These seasonal restrictions on food type availability can undoubtedly affect animal food choice. For example, Japanese macaques (*Macaca fuscata*) consume fruit and seeds in autumn while the consumption of fibrous foods such as leaves and stems dominates their diet in spring (Hanya et al. 2003). Similarly, Francois langurs (*Trachypithecus francoisi*) feed upon different food types during different seasons due to availability shifts (Zhou et al. 2006). Animals are not always notably affected by changes in food type availability, however. No changes occurred in the number of fruit species found in chimpanzee (*Pan troglodytes schweinfurthii*) faeces during the fruiting and non-fruiting seasons or in areas differing in fruit availability, for example (Yamagiwa & Basabose 2006).

Furthermore, orang-utans (*Pongo pygmaeus*) only consumed abundant foods when their preferred foods were in shortage (Leighton 1993). How various species respond to plant phenological changes is of interest as there are apparent differences in responses. Furthermore, whether differences in use of available food types exists between conspecifics differing in age, sex, or reproductive status remains to be determined for many species.

One reason that animals do not always choose foods based on availability is that foods' nutritional content also effects animal food choice (Lambert & Rothman 2015). Studies in nutritional ecology have revealed the nutritional basis of foraging, food choice, and preference in animals both in the laboratory (Lee et al. 2008; Raubenheimer & Simpson 1997) and the wild (Johnson et al. 2013; Milton 1981; Nie et al. 2015; Oates et al. 1980; Rothman et al. 2011b; Waterman 1984). Recent studies on primate nutritional ecology reveal that many animals seek to consume a balance of different nutrients and, when ecologically constrained from doing so, engage complex nutritional priorities (Raubenheimer & Simpson 1997). A striking example of maintaining a particular nutrient ratio during free-ranging foraging was demonstrated in a study of a female chacma baboon (*Papio hamadryas usinus*) who selected food combinations in proportions that maintained a remarkably constant dietary available protein to non-protein energy ratio for thirty consecutive days, despite this macronutrient ratio not being found in natural food items (Johnson et al. 2013). Similarly, macronutrients (protein, carbohydrates, fat) were regulated at a specific balance by domestic dogs and cats suggesting

specific macronutrient intake targets (Hewson-Hughes et al. 2013; Hewson-Hughes et al. 2011).

In circumstances where constraints on food availability prevent such macronutrient balancing, some primates have been found to prioritize the acquisition of a required amount of certain nutrients. This means that the animals maintain a relatively stable daily intake of the prioritized nutrient while allowing the intake of other nutrients to vary with the nutrient composition of available foods. For example, Peruvian spider monkeys (*Ateles chamek*) (Felton et al. 2009b) and humans (*Homo sapiens sapiens*) (Gosby et al. 2013; Martinez-Cordero et al. 2012; Raubenheimer et al. 2015) prioritize protein energy intake while mountain gorillas (*G. beringei*) prioritize non-protein energy intake (Rothman et al. 2011b).

Factors such as sex, age, and physiological status can also influence animal food and nutrient intake patterns. For example, the dietary requirements of juveniles are expected to surpass those of adults (per body mass) due to the nutrients and energy required for a growing body (National Research Council 2003). This has been confirmed in mountain gorillas (*G. beringei*) as juveniles consume more minerals per unit of metabolic body mass than adults and more protein per unit of body mass than adult males (Rothman et al. 2008b).

Different nutrient requirements are also expected between females and males (and between females at different points of their reproductive cycle) due to pregnancy, lactation (Clutton-Brock et al. 1989; National Research Council 2003; Picciano 2003; Rothman et al.

2008b; Strier 2000) and the energetic demands of infant carrying (Tobey et al. 2006). Both foetal and infant development necessitate increased nutritional intake by the mother (Picciano 2003), likely affecting food and nutrient intake during pregnancy and lactation. When compared with adult males, adult female mountain gorillas (*G. beringei*) consume more food and more protein per metabolic body mass (Rothman et al. 2008b), reflecting their increased energetic demands. However, such sexual differences in nutrient intake patterns were not found in Peruvian spider monkeys (*A. chamek*) (Felton et al. 2009b). Furthermore, lactating and pregnant female chimpanzees (*Pan troglodytes schweinfurthii*) consumed higher quality foods than those who were not (Murray et al. 2009), male and lactating female ring-tailed lemurs (*Lemur catta*) differed in their food consumption (O'Mara & Hickey 2014), and greater energy intake and feeding rates have been described in lactating females compared with those who were pregnant or cycling in wild white-headed capuchins (*Cebus capucinus*) (McCabe & Fedigan 2007). The costs of infant carrying are also expected to affect female nutritional requirements. A study on yellow baboons (*Papio cynocephalus*) estimated that a mother requires an additional 5% of her energy intake to carry her baby for its first month of life (Altmann & Samuels 1992). Furthermore, primates that carry their offspring tend to have smaller home ranges and decreased daily travel distances relative to species who leave their infants in a tree or nest (Ross 2001), suggesting these animals compensate for the extra energetic expense through a reduction in activity levels. Similar trends occur within species.

For example, female Sumatran long-tailed macaques (*Macaca fascicularis*) who have infants reduce their foraging range and activity compared with females who do not have infants (van Schaik & Maria 1986).

This study aims to investigate food choice and nutrient intake of the golden snub-nosed monkey (*Rhinopithecus roxellana*) during two seasons of clear differences in food availability (Guo et al. 2007). This was conducted to determine if and how food and nutrient intake patterns vary according to seasonal availability and if age, sex, and female reproductive status affect nutrient intake patterns in this species. The golden snub-nosed monkey is an endangered Colobine endemic to China (IUCN 2015) and is highly dimorphic with adult males weighing 16.81 ± 0.41 kg, adult females weighing 9.72 ± 0.31 kg, and juveniles weighing 5.85 ± 0.58 kg (Guo, S. pers. com.). This species occupies broadleaf, conifer, and mixed broadleaf/conifer forests in mountain ranges in central and north-western China at altitudes ranging from 1,500 to 3,300 m above sea level (Hu 1998; Renmei et al. 1998) and is subjected to seasonal changes in food availability (Guo et al. 2007). Reproduction in this species is seasonal with copulation occurring all year but conception only occurring in autumn (Qi et al. 2008). As most infants are born between March and May (Qi et al. 2008), lactation begins in late spring and continues through summer and into autumn. These monkeys travel relatively long distances per day compared with other colobine monkeys and have large home ranges (Kirkpatrick & Grueter 2010). One troop in the Qinling Mountains, for example, has a home range of 18.3 Km^2 and

has daily path lengths ranging from 0.75 to 5 Km (Tan et al. 2007). This can result in high energy expenditure in infant carrying females.

Golden snub-nosed monkeys have a complex multi-level society (Qi et al. 2014). Multiple troops may inhabit similar areas and each troop is made up of solitary males, all male units (AMU), which consist of adult and sub-adult males, and multiple one male units (OMU) which consist of an adult male, multiple adult females, and their offspring (Grueter 2013; Qi et al. 2014). AMUs and solitary males spend most of the time separate from the band of OMUs (Qi et al. 2014). Males from an AMU may try and replace a male in an OMU or may attract females from multiple units and form a new OMU (Yao et al. 2011). A dominance hierarchy exists both between and within OMUs and both competition over and monopolization of access to popular food sources occur in this species (Li et al. 2005; Zhang et al. 2008b). Within OMUs, the dominance order is linear and the duration of an OMU's stay in the troop is positively associated with the OMU's rank (Zhang et al. 2008b). Both males and females disperse between OMUs (Chen 1983; Zhang et al. 2008a; Zhang et al. 2006b; Zhao et al. 2008) and an inter-troop dispersal has also been observed (Zhang et al. 2008a).

Golden snub-nosed monkeys are foregut fermenters and consume a diet which consists of a large proportion of leaves (Caton 1998). In addition to leaves, these monkeys consume seeds, bark, fruit (Guo et al. 2007; Li 2006; Li 2007; Li et al. 2010), and occasionally invertebrates (Li et al. 2002; Yang et al. 2016) and birds (Zhao 2008). Lichenivory occurs in

some populations (Guo et al. 2007; Li 2006; Liu et al. 2013) but not in others (Li et al. 2010). Although snub-nosed monkeys consume seeds, it is unlikely that they are seed dispersers as many seeds are masticated and thus destroyed when consumed (pers. obs.). Other colobine monkeys, such as the black colobus monkey (*Colobus satanus*) (McKey et al. 1981), break seeds during consumption. Colobines are thus not expected to be key seed dispersers (Corlett & Lucas 1990).

This species has been observed to consume nearly 100 different plant species across different parts of its range (Guo et al. 2007; Li et al. 2010; Li et al. 2002; Liu et al. 2013; Yiming 2006). A troop inhabiting a nature reserve in Hubei province selected plant parts that are high in water soluble carbohydrates (WSC) and low in fibre (Liu et al. 2013). Lichens, an important component of this population's diet, contain high levels of WSC, similar amounts of lipids, and low levels of protein and fibre compared to most plants parts (Liu et al. 2013). Furthermore, it is not known whether age, sex, or reproductive status affect foraging behaviour or nutrient intake in this species. This is of interest as these factors are expected to influence energetic requirements (Amato et al. 2014; National Research Council 2003; Rothman et al. 2008b). We can thus expect differences in both foraging behaviour and nutrient intake based on these factors.

The following questions are addressed in this study: 1) what plant species are consumed by this snub-nosed monkey troop and does plant species consumption reflect plant species

availability? As their food choice is expected to be primarily influenced by nutrient requirements, I predicted their food intake to be independent of relative abundances of food items in their habitat; 2) Do this troop's foraging patterns differ between summer and autumn? Despite being influenced by nutritional requirements, I predicted this troop's food intake to change seasonally due to phenological induced restrictions on food availability 3) Does this troop's nutrient intake differ between summer and autumn? I predicted these monkeys' nutrient intake would be influenced by nutritional requirements and thus did not expect the composition of their nutrient intake to reflect seasonal trends in nutrient availability 4) Do food (plant species and food type) and nutrient intake differ by age, sex, and reproductive status? Due to expected differences in nutrient and energetic requirements, I predicted: a. Food and nutrient intake patterns to differ between adults and juveniles due to greater energetic demands of juveniles (per kg of metabolic body mass); b. Food and nutrient intake patterns to differ between males and females due to females having greater energetic demands (per kg of metabolic body mass) associated with pregnancy, lactation, and infant carrying; c. Food and nutrient intake patterns to differ between lactating and non-lactating females due to lactation being the most energetically demanding female physiological status.

2.3 Methods

2.3.1 Study site and focal animals

This study was conducted in Zhouzhi National Nature Reserve (108°16'E, 30°50'N), Shaanxi Province, China (Figure 2.1). Established in 1985, the reserve covers an area of 53,000

ha (Zhao & Li 2009). Deciduous broadleaf forest is found from 1,400 m to 2,200 m, mixed deciduous broadleaf and conifer forest from 2,200 m to 2,600 m, and above 2,600 m, it is exclusively conifer forests (Li et al. 2000). There are two troops of golden snub-nosed monkeys inhabiting this area. The West Ridge Troop (WRT) of Zhouzhi National Nature Reserve, which inhabits altitudes ranging from 1,500 to 2,750 m above sea level (Li et al. 2000), was the focal troop in this study. This troop, which has approximately 175 members, has been the subject of long-term ecological and behavioural studies and is thus habituated to the presence of researchers. This troop is provisioned over winter by other students. As my observations did not commence until summer, the troop's feeding behaviour should not have been seriously impacted by the provisioning.

2.3.2 Vegetation Survey

Vegetation surveys were conducted along three 40m line transects in each of the thirteen main feeding areas that the monkeys utilized during both seasons, with the direction of transect randomly selected from the centre of the feeding area. Such feeding areas were defined as areas where the troop stopped to feed for an extended period. Areas where a small amount of food (e.g. a handful of leaves) was consumed by a monkey while moving through were not included. Transects included all identifiable plant species and were conducted once during the relevant season. At every 4 meters along each 40 metre transect, the species and the diameter at breast height (DBH) of any plant that intersected the transect at ground level, 2 meters high, 4 meters high, and the canopy was recorded. Each recorded plant was assigned to

one of the following categories based on age (for saplings) or DBH: 1 (saplings), 2 (DBH < 39.9 cm), 3 (40.0 cm < DBH < 79.9 cm), 4 (DBH > 80.0 cm). As DBH has been demonstrated to be an accurate method to measure fruit abundance and is a beneficial method to use in studies with time constraints (Chapman et al. 1992), it was used to estimate general, non-food type specific, plant availability.

2.3.3 Focal Animal Identification

Data were collected from the following subsets of the focal group:

Non-lactating females (NLF): females who are sexually mature but who were not lactating. Sexual maturity was indicated by breast and nipple size and/or by engaging in sexual behaviour.

Lactating female (LF): females who are sexually mature and who are breast feeding an infant.

Adult male (AM): males who are sexually mature as indicated by their size and the presence of granulomatous flanges on both corners of their upper lips.

Juvenile (J): individual who is weaned and thus feeding on solid foods but who is not yet sexually mature. Infants were not included in this study.

2.3.4 Feeding Data Collection

Data were collected from June to August of 2011 (summer) and during October of 2012 (autumn) and the troop was followed for approximately 6,251 minutes (4,511 minutes in summer, 1,740 minutes in autumn). Observations during winter and spring or across multiple

years were not possible due to various constraints (e.g. time and financial constraints, studies on the same troop by other students). This limitation impedes my ability to investigate seasonality to its fullest extent in this troop and to investigate interannual trends in food availability and consumption, which can be highly variable (e.g. Chapman et al. 2005). This troop can still be studied across these two seasons, however, allowing for a description of their nutritional ecology across this specific time frame.

Animals were typically followed and observed between 0800 and 1700 hours with the number of observation days per week varying depending on factors such as weather conditions and guide availability. There was some variation in the observational hours, however, as the troop could not always be located immediately in the morning or because of inclement weather. As this troop is well habituated to human presence, they can be observed from short distances (as close as a few meters or from the base of their feeding tree). Movement through the troop's feeding area was minimized to reduce disturbances, however, so the observation distance typically varied from a few metres to 8 metres. Scans were conducted to collect feeding data with scans beginning with the first feeding individual that was spotted and continuing in a clockwise manner through the rest of the troop. During each scan, focal animal sampling (Altmann 1974) was used to collect data from a single individual for a maximum of 10 minutes or until he/she stopped eating for 30 seconds, left the feeding area, or changed to another activity (e.g. grooming, playing, sleeping). This 10-minute maximum time frame is defined as



Figure 2.1 The location of the study site, Zhouzhi National Nature Reserve ($108^{\circ}16'E$, $30^{\circ}50'N$).

a ‘feeding bout’ and is the sampling unit. During each observed feeding bout, the food item (fruit (includes pulp and seeds if whole item consumed), bark, leaves, seeds, or fungal fruiting body), the food species, and the number of food items consumed were recorded. Once the feeding bout ended, or the focal animal went out of view for more than 30 seconds, the scan continued until another feeding individual was spotted. To estimate the weight consumed of each food item (e.g. a leaf or a piece of fruit), representative samples of food items that were observed to be eaten were collected once the monkeys left the area and an average weight of each item was calculated. Samples of consumed plants and/or photographs of the plants were

collected for identification purpose. Plants were identified with the assistance of Dang Gaodi, Guo Songtao, and Li Baoguo. For plants not identifiable, the local name is used.

2.3.5 Food Sample Collection

When possible, samples were collected from all food items and were collected from the same individual plant upon which the monkeys fed. However, sometimes with smaller food plants such as herbs or saplings, all leaves would be consumed by the monkeys or individual plants would not always be able to supply the amount of sample required (~ 100 g dry weight). In such cases, samples were collected from multiple individuals of the same species and mixed. The large amount of sample required for all food items also necessitated combining foods differing in maturity (e.g. young and mature leaves from a species) as not enough young leaves were available to make up the required amount. As observations began in late June and there were hence not many feeding events on young leaves (only 2 events), this should not majorly impact the overall findings of the study. This limitation needs to be considered, never the less, as mature and immature leaves are known to differ in nutrient content and digestibility (e.g. McKey et al. 1981). For fruits that were consumed whole, the whole fruit, including pulp and seeds, were dried and analysed together. If seeds were removed by the monkeys and were the only part consumed, seeds were removed during sampling and analysed as such. For foods consumed during both early and late summer, samples were collected and separated for these respective times to reflect temporal changes in nutrient composition. Autumn foods, while analysed, were not divided into ‘early and ‘late’ season as the autumn observational period was

shorter in duration. Samples were dried in an oven at ~60°C or in a food dehydrator, stored in sealable plastic bags, and then re-dried at 105°C prior to nutrient analyses. As the drying temperature is above the recommended temperature of ~55°C (Rothman et al. 2011a), the possibility of an overestimate of fibre and underestimate of soluble sugars should be considered. All samples were analysed for nutritional content at Northwest University (Xi'an, China).

2.3.6 Nutrient Analyses

For nutrient analyses, all samples were ground using a 1mm mill and were analysed in triplicate. For determination of the crude protein (CP) content of food items, total nitrogen was determined using the Kjeldahl procedure (using a BUCHI, K-360) and nitrogen values were multiplied by 6.25 to estimate the CP content (Maynard & Loosli 1969; van Soest 1994). A petroleum ether extract (FOSS ST310, Shanghai) was used to determine the crude lipid content of food items (Conklin-Brittain et al. 2006). Neutral detergent fibre (NDF), acid detergent fibre (ADF), and lignin content were determined sequentially using the ANKOM A2000i FiberAnalyzer. Samples were assayed for neutral detergent fibre with residual ash (with sodium sulfite and α -amylase), then for acid detergent fibre with residual ash, and finally for lignin (Van Soest et al. 1991; Rothman et al. 2008b). Water soluble carbohydrate (WSC) content was determined using the Anthrone method while Fehling's solution and 1% hydrochloric acid hydrolysis were used to determine the starch content of food items (Lawler et al. 2006). During

statistical analysis, the starch and WSC content of the food items were combined and referred to collectively as non-structural carbohydrates (NSC).

2.3.7 Data Analysis

To determine the relationship between food availability and food choice, an availability index (AI) of each food species was derived using the following formula:

$$AI = \sum_i^n SC_i * N_i$$

Where SC_i = size class i and N_i = the number of plants in the size class i . This index, taking into account both tree size and abundance, was used to describe the availability of plant species within this troop's environment. To derive the troop's food choice, the proportional contribution (PC) of each food item was calculated by the following:

$$PC = GC_i / TGC$$

Where GC_i = grams consumed of food item i by all troop members collectively and TGC = total grams of food consumed by the troop. Each food item's proportional contribution was ranked while maintaining the relative differences between the proportional contributions of each food item. As how the troop as a whole responds to food availability in their habitat was of interest, the feeding bouts of all troop members were utilized in this analysis and variation between subsets of the troop was not investigated.

To determine whether food species consumption differs between summer and autumn, the proportion of observations in which a plant species was consumed during each season was calculated for each subset (juveniles, adult males, lactating females, non-lactating females).

Only plants species identifiable by Latin name or local name were used in this analysis. Five of the 39 plant species observed to be consumed during this study were not identifiable by Latin or local name and were thus excluded from this analysis and from the plant availability analysis. These five species made up 2% of the total observations. Similarly, the proportion of observations in which a food type was consumed during summer and autumn was calculated for each subset to investigate food type consumption across two seasons.

To test the effect of seasonal nutrient availability on the nutrient intake patterns of the focal animals, the proportional contribution of each analysed nutrient (CP, lipids, NSC, NDF, and lignin) to each food item was determined for both summer (n=26) and autumn (n=33) as was the proportional contribution of each nutrient to the troop's feeding bouts during the two seasons. The proportional contributions of analysed nutrients to each bout were used instead of absolute amounts to compensate for the fact that feed bouts varied in duration. Nutritional data were unavailable for one food item, *Corylus ferox*, due to missing samples. This species made up 0.3% of the observed diet by weight. The average nutritional content of two closely related food items, *Corylus heterophylla* and *Corylus chinensis*, was used as an estimate for this food item.

To test the effect of age, sex, and physiological status on food intake, the proportion of observations in which a plant species was consumed was calculated for each subset (adults and juveniles; males and females; lactating females and non-lactating females). As above, only

plants species identifiable by Latin name or local name were used in this analysis. The proportion of observations in which a food type was consumed was calculated for each subset to determine whether food type consumption varies with age, sex, and/or reproductive status. Feeding events including species that could not be identified by Latin or local name were included in this analysis.

To test the effect of age, sex, and reproductive status on nutrient intake, the proportional contribution of CP, lipids, NSC, NDF, and lignin, to each feeding bout were compared. As food and nutrient intake are strongly determined by an animal's size (Nagy 2005), the proportional contribution of each feeding bout was divided by an estimated metabolic body mass ($M^{.762}$) (Rothman et al. 2008b) of the feeding individual. Because the weights of our focal animals could not be obtained, we used an average weight for each age and sex group which was collected from members of this troop during other studies. The following weight estimates were used: adult female: 9.72 kg; adult male: 16.81 kg; juvenile: 5.85 kg (Guo, S. pers. com.). The following equation was used to calculate each nutrient's proportional contribution to each animal's feeding bout:

$$PI_i = (P_i / \sum_i^n P_i) / M$$

where PI_i is the proportional intake of nutrient i , P_i is the proportional contribution of nutrient i for n number of analysed nutrients, and M is the animal's estimated metabolic body mass.

Spearman's rank correlation (IBM SPSS 21) was used to test for a correlation between food species' AI and contribution to the troops' diet. The Mann-Whitney U test (SPSS version 22) was used to test for differences in food species and food type choice between summer and autumn for each subset. The Kruskal-Wallis test (SPSS version 22) was used to test for differences in food species and food type choice between subsets within each of the two seasons. For these tests, different parts of the same food species were considered to be different food items (e.g. leaves and fruit of *Lindera obtusiloba* were two different foods). PERMANOVA (permutational multivariate analysis of variance) (PERMANOVA+; Primer6) was used to test for seasonal differences in the nutrient composition of food items and for seasonal differences in the proportional contribution per bout of the troop as a whole. Both PERMANOVA and General Linear Model (GLM) (IBM SPSS 22) were used to test for differences in the nutritional proportional contribution between subsets of the troop based on sex, age, and female reproductive status, allowing for comparison of the two tests. PERMANOVA is a non-parametric method of analysing multivariate data which uses permutations to determine P-values (Anderson 2001). The independence and similar distribution of observations are the only assumptions of this method (Anderson 2001). GLM is also a multivariate statistical method and has the following assumptions: the errors of observations and the independent variables are independent, constant covariance of dependent variables across cells, and a multivariate normal distribution of the errors across the dependent

variables (although the method is robust to deviations from this assumption) (IBM SPSS 22). For all analyses conducted using PERMANOVA, the Euclidean distance was used in production of the resemblance matrix and all data were square root transformed prior to production of the resemblance matrix. In the PERMANOVA results, the between cluster variance to within cluster variance ratio is described by the pseudo-f statistic (Caliński & Harabasz 1974). Thus, greater values for this statistic reflect greater separation between groups. For GLM tests, the Tukey post hoc analysis was conducted to determine where differences occurred in the comparisons between proportional nutrient intake in different subsets of the troop.

2.4 Results

2.4.1 Golden Snub-nosed Monkey Foods

The foods of this troop came from 35 plant families (the families of seven unidentifiable foods are unknown, however). Twenty-seven different plant species were consumed by the focal animals during summer and 32 plant species and one fungal species were consumed during autumn. Five food species made up at least 5% of the troop's diet by weight during summer. Similarly, five plant species made up at least 5% of their diet during autumn. One plant species, *Morus alba* (Family: *Moraceae*), was the main contributor to the troop's diet during both summer (36.5%) and autumn (27.4%).

The proportional nutritional composition of the troop's main foods (those that made up at least 5% of their diet) and their contribution to the troop's diet are listed in Table 2.1. A

comprehensive list including the proportional nutrient composition of all species consumed is in Appendix I, Table A1.1. The main contributors to this troop's diet do not occupy a similar area in nutrient space (i.e. do not have a similar nutrient balance) when proportional crude protein (CP), non-protein (NP) (lipids and non-structural carbohydrates) and neutral detergent fibre (NDF) are visualized (Figure 2.2). Eight main foods are found on the outer ranges of the nutrient space occupied by all foods, however. Looking at individual nutrients instead of the balance of all three, 3 of the main foods are low in CP, 2 are high in CP, 2 are high in NP, 5 are low in NDF, and 1 is high in NDF when comparing main dietary contributors with remaining foods (Figure 2.2).

2.4.2 Seasonal Effect of Availability on Food and Nutrient Intake

This troop did not select food species based on species' availability during summer (n=23, Spearman's rho: -.175, P=0.415, R²=0.0092) or autumn (n=29, Spearman's rho: -.396, P=0.030, R²=0.0669). If five outliers are removed (two foods with high dietary rank scores and three foods with high availability scores) from the data, however, the relationship does not reach significance in either summer (n=22, Spearman's rho: -.336, P=0.127, R²=0.0174) or autumn (n=25, Spearman's rho: -.231, P=0.267, R²=0.0424) (Figure 2.3). Correlations remain negative during both seasons, however. The availability index scores of identified food species are listed in Table 2.2.

Summer foods (n=28) had a greater proportion of CP (Pseudo-F=6.265; df=27; P=0.015) and lipids (Pseudo-F=8.1226; df=27; P=0.003) and a smaller proportion of NSC

(Pseudo-F=18.849; df=27; P=0.001) than autumn foods (n=39). Summer and autumn foods did not differ in their proportional NDF (Pseudo-F=0.56956; df=27; P=0.458) or lignin content (Pseudo-F=6.7329E⁻⁵; df=27; P=0.994). The troop's feeding bouts had a significantly greater proportional contribution of CP (Pseudo-F=34.918; df=507; P=0.001), lipids (Pseudo-F=103.52; df=507; P=0.001), lignin (Pseudo-F=11.159; df=507; P=0.001), and a significantly smaller proportional contribution of NSC (Pseudo-F=190.68; df=507; P=0.001) and NDF (Pseudo-F=19.979; df=507; P=0.001) during summer (n=366) than autumn (n=142). The average proportional contribution of nutrients to the troop's food items and nutrient intake are listed in Table 2.3.

Table 2.1 The proportional nutritional composition of foods that made up at least 5% of the troop's diet (by weight) during summer and autumn. Note: *Morus alba* was consumed and thus nutritionally analysed during early summer, late summer, and autumn and thus appears three times in the table.

Species	Part	%CP	%Lipids	%NSC	%NDF	%Lignin	% of Diet	Season
<i>Morus alba</i>	leaves	30.4	6.5	17.5	42.3	3.3	36.5	Late Summer
<i>Morus alba</i>	leaves	27.0	3.3	15.8	41.9	11.9	36.5	Early Summer
<i>Morus alba</i>	leaves	20.7	2.2	25.1	36.0	16.0	27.4	Autumn
<i>Litsea rubescens</i>	fruit	12.5	22.2	13.8	35.0	16.6	18.0	Summer
<i>Quercus aliena</i>	seeds	4.4	0.9	54.4	38.9	1.5	16.3	Autumn
<i>Cornus spp</i>	fruit	12.2	7.0	11.4	49.6	19.8	13.5	Summer
<i>Pinus massoniana</i>	seeds	3.7	8.0	8.1	60.7	19.5	11.4	Autumn
<i>Lindera obtusiloba</i>	fruit	8.4	34.4	9.7	28.1	19.5	9.8	Summer
<i>Crataegus cuneata</i>	fruit	4.1	7.9	27.9	45.2	14.9	8.4	Summer
<i>Prunus armeniaca</i>	leaves	17.1	6.4	24.6	49.3	2.6	7.8	Autumn
Unidentified Fungus	fruiting body	12.7	1.0	20.0	57.3	9.1	5.8	Autumn

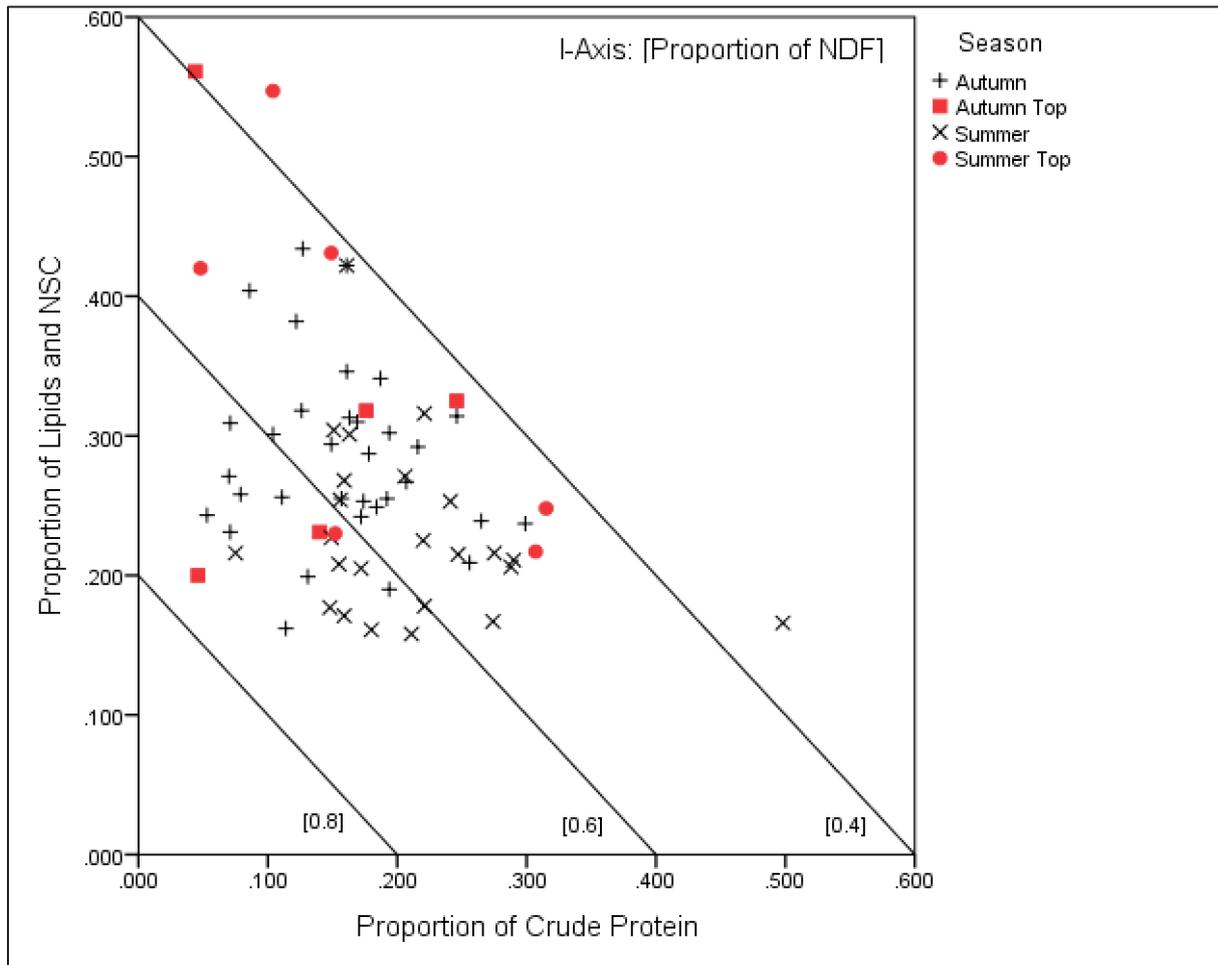


Figure 2.2 The proportional crude protein, lipid and non-structural carbohydrate (NSC), and neutral detergent fibre (NDF) composition of the top foods (at least 5% of the troop's diet by weight) during summer (red circles) and autumn (red squares) compared with remaining foods (summer (x) and autumn (+)). The implicit axis, with values given in brackets, runs inverse to the x axis. The proportional NDF content is thus found by determining where the isoline passing through the relevant point intercepts the x-axis, and subtracting the x-value of that point from 1.

Table 2.2 The availability index score of food species identified by Latin name or, if unidentifiable, local name during summer and autumn. * Main dietary food items.

Summer		Autumn	
Species	Availability Score	Species	Availability Score
Ji Liu	334	Qing Gang Mu	736
<i>Litsea rubescens</i> *	260	<i>Acer mono</i>	99
<i>Corylus ferox</i>	184	<i>Litsea rubescens</i>	83
<i>Grewia biloba</i>	124	<i>Toxicodendron vernicifluum</i>	63
<i>Ulmus macrocarpa</i>	91	<i>Corylus heterophylla</i>	49
Qing Liang Zi	71	<i>Salix spp</i>	38
<i>Salix matsudana</i>	46	<i>Ulmus macrocarpa</i>	36
<i>Morus alba</i> *	31	<i>Deutzia vilmorinae</i>	27
<i>Stachyurus chinensis</i>	28	<i>Glechoma longituba</i>	25
<i>Padus asiatica</i>	23	<i>Pinus massoniana</i> *	19
<i>Corylus chinensis</i>	20	<i>Padus spp</i>	16
<i>Deutzia vilmorinae</i>	19	Qing Liang Zi	12
<i>Corylus heterophylla</i>	15	<i>Padus asiatica</i>	10
<i>Fraxinus mandshurica</i>	12	<i>Schisandra chinensis</i>	10
<i>Meliosma cuneifolia</i>	10	<i>Salix matsudana</i>	9
<i>Prunus salicina</i>	6	Ma Huan Shao	6
<i>Prunus armeniaca</i>	5	<i>Malus baccata</i>	6
<i>Actinidia eriantha</i>	4	<i>Celastrus orbiculatus</i>	4
<i>Celastrus orbiculatus</i>	0	<i>Prunus salicina</i>	4
<i>Lindera obtusiloba</i> *	0	<i>Grewia biloba</i>	3
<i>Cornus spp</i> *	0	<i>Actinidia eriantha</i>	1
<i>Quercus aliena</i>	0	<i>Swida macrophylla</i>	0
<i>Prunus pleiocerasus</i>	0	Unidentified Mushroom*	0
<i>Crataegus cuneata</i> *	0	<i>Ulmus bergmanniana</i>	0
		Huang Bo	0
		Ku Dong Po	0
		<i>Quercus aliena</i> *	0
		<i>Morus alba</i> *	0
		<i>Fraxinus mandshurica</i>	0
		<i>Prunus armeniaca</i> *	0

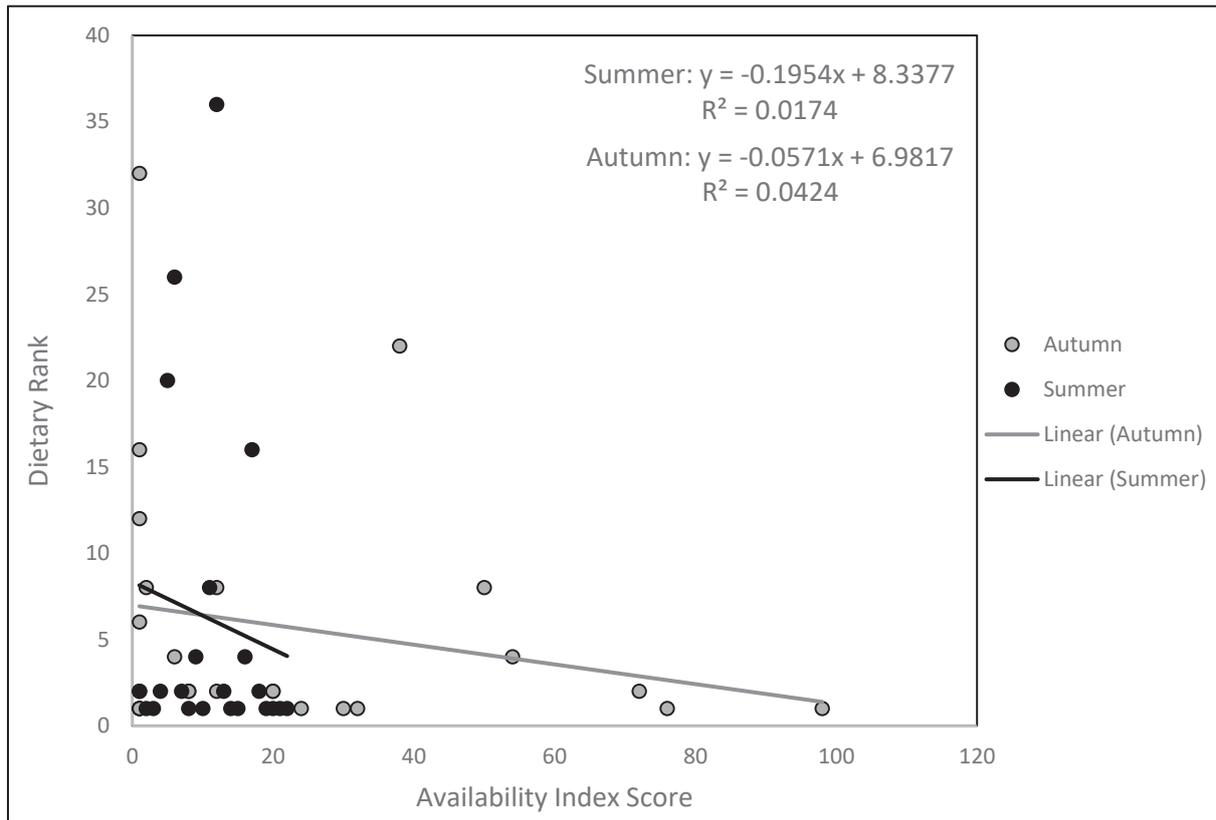


Figure 2.3 The relationship between the availability index of plant species and the plant species' rank based on its proportional contribution to the troop's diet (grams consumed of species/total grams consumed) with linear trendlines (Summer: $n=22$, Spearman's ρ : -0.336 , $P=0.127$; Autumn: $n=25$, Spearman's ρ : -0.231 , $P=0.267$). Note: 5 outliers have been removed.

Table 2.3 The average proportional contribution of nutrients (\pm standard error) to the troop's food items and the troop's nutrient intake (diet) during summer and autumn. CP=crude protein, NSC=non-structural carbohydrates, NDF=neutral detergent fibre, AL=acid lignin.

	CP	Lipids	NSC	NDF	AL
Summer Foods	0.134 \pm 0.009	0.065 \pm 0.015	0.120 \pm 0.008	0.362 \pm 0.016	0.123 \pm 0.012
Autumn Foods	0.108 \pm 0.007	0.031 \pm 0.005	0.177 \pm 0.012	0.410 \pm 0.022	0.142 \pm 0.016
Summer Diet	0.034 \pm 0.001	0.025 \pm 0.001	0.026 \pm 0.001	0.085 \pm 0.002	0.032 \pm 0.001
Autumn Diet	0.025 \pm 0.001	0.008 \pm 0.001	0.044 \pm 0.002	0.086 \pm 0.002	0.027 \pm 0.001

2.4.3 The Effect of Age, Sex, and Reproductive Status on Food Choice

Food choice in terms of species consumed did not differ between individuals of different sex, age, or reproductive status within either season ($P > 0.05$ for all) or within subsets between seasons ($P > 0.05$ for all) (Appendix 1, Table A1.2). This troop consumed the following food types: leaves, fruit, bark, seeds, and fungal fruiting body (Figure 2.4). No statistically significant differences were detected in the choice of food types between the subsets during either season ($P = 0.392$ for all) or between seasons for any of the subsets ($P = 0.317$ for all except for leaf consumption by lactating females: $P = 1.000$).

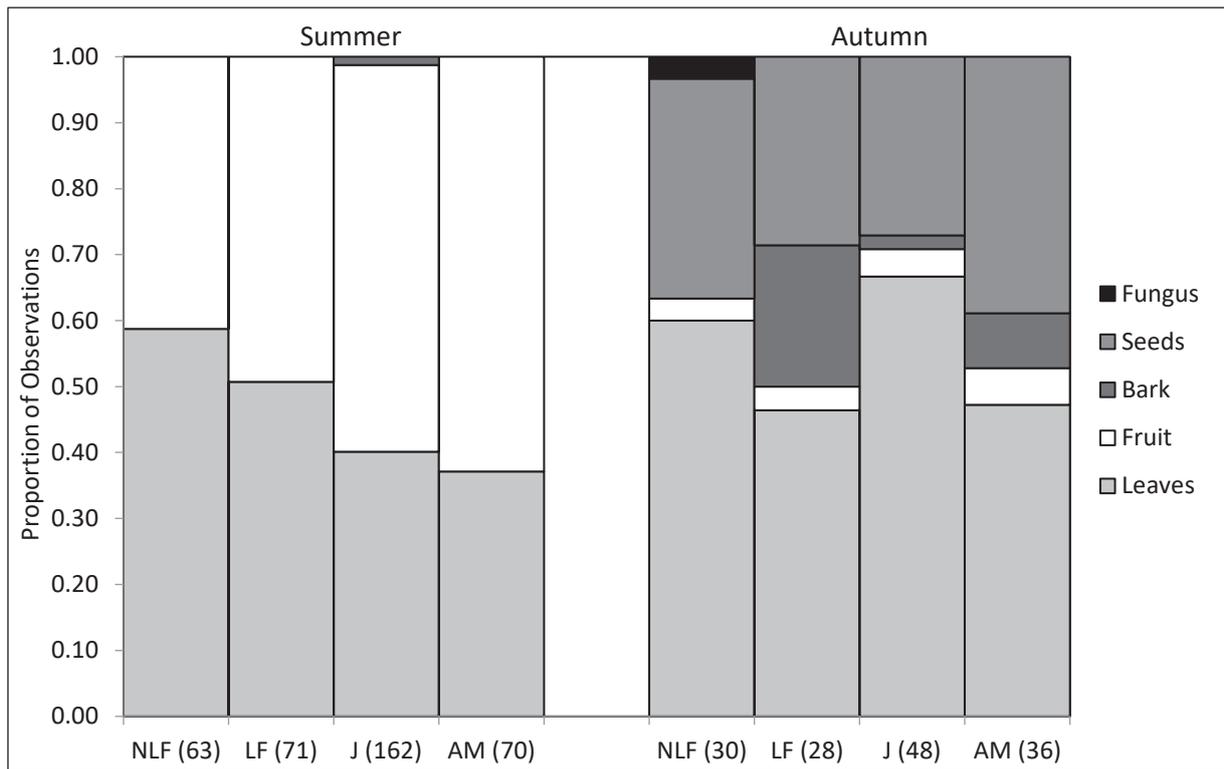


Figure 2.4 The proportion of observations for each subset of the troop (NLF=Non-lactating Females, LF= Lactating females, AM=Adult Males, J=Juveniles) in which individuals consumed the following: leaves, fruit, bark, seeds, fungus during summer and autumn. Numbers in parentheses are the number of observations for each subset.

2.4.4 Nutrient Intake of Juveniles vs. Adults

During summer, the juvenile diet (n=162) had a significantly greater proportional contribution of all tested nutrients per Kg of metabolic body mass than that of adult monkeys (n=204). These significant differences were detected by both statistical methods: PERMANOVA (CP: (Pseudo-F=74.428; df=365; P=0.001), lipids (Pseudo-F=21.866; df=365; P=0.001), NSC (Pseudo-F=327.3; df=365; P=0.001), NDF (Pseudo-F=433.91; df=365; P=0.001), and lignin (Pseudo-F=195.56; df=365; P=0.001)) ; GLM: (CP (P=0.000), lipids

(P=0.000), NSC (P=0.000), NDF (P=0.000), and lignin (P=0.000)). The same trend was observed in autumn (juveniles: n=48; adults: n=94). PERMANOVA: (CP: Pseudo-F=33.201; df=141; P=0.001; Lipids: Pseudo-F=15.362; df=141; P=0.001; NSC: Pseudo-F=38.354; df=141; P=0.001; NDF: Pseudo-F=135.92; df=141; P=0.001; lignin: Pseudo-F=22.21; df=141; P=0.001) and GLM: (CP (P=0.000), lipids (P=0.000), NSC (P=0.000), NDF (P=0.000), and lignin (P=0.000)). The average proportional amount consumed per feeding bout for juveniles and adults (per Kg of metabolic body mass) are presented in table 2.4 while the average amounts consumed in absolute terms are presented in table 2.5.

2.4.5 Nutrient Intake of Adult Females vs. Adult Males

During summer, both statistical tests detected a significantly greater proportional contribution of CP, NSC, NDF, and AL to the female diet (n=133), per Kg of metabolic body mass, than to that of males (n=71): PERMANOVA: (CP (Pseudo-F=46.15; df=203; P=0.001), NSC (Pseudo-F=122.06; df=203; P=0.001), NDF (Pseudo-F=173.59; df=203; P=0.001), lignin (Pseudo-F=58.747; df=203; P=0.001), lipids (Pseudo-F=3.6421; df=203; P=0.056); GLM: (CP (P=0.000), NSC (P=0.000), NDF (P=0.000), lignin (P=0.000), lipids (P=0.462)).

Table 2.4 The average proportional nutrient intake per feeding bout (g per Kg of metabolic body mass) \pm the standard error for all subsets during summer (top value) and autumn (bottom value). N is the number of feeding bouts observed for each subset during summer (top) and autumn (bottom). NSC=non-structural carbohydrates, NDF=neutral detergent fibre, AL=acid lignin.

	Crude Protein	Lipids	NSC	NDF	AL
Juvenile (N=162/48)	0.042 \pm 0.002	0.032 \pm 0.002	0.034 \pm 0.001	0.111 \pm 0.002	0.042 \pm 0.001
	0.036 \pm 0.003	0.011 \pm 0.001	0.062 \pm 0.005	0.115 \pm 0.003	0.037 \pm 0.002
Adults (N=204/94)	0.027 \pm 0.001	0.020 \pm 0.001	0.020 \pm 0.000	0.064 \pm 0.001	0.024 \pm 0.001
	0.019 \pm 0.001	0.006 \pm 0.000	0.035 \pm 0.002	0.071 \pm 0.002	0.022 \pm 0.001
Adult Females (N=133/58)	0.031 \pm 0.001	0.022 \pm 0.002	0.023 \pm 0.000	0.073 \pm 0.001	0.027 \pm 0.001
	0.022 \pm 0.002	0.007 \pm 0.001	0.038 \pm 0.003	0.082 \pm 0.002	0.027 \pm 0.002
Adult Males (N=71/36)	0.019 \pm 0.001	0.016 \pm 0.002	0.016 \pm 0.000	0.047 \pm 0.001	0.018 \pm 0.001
	0.014 \pm 0.002	0.005 \pm 0.001	0.029 \pm 0.003	0.054 \pm 0.002	0.015 \pm 0.001
Non-lactating Female (N=62/30)	0.032 \pm 0.002	0.022 \pm 0.003	0.023 \pm 0.001	0.073 \pm 0.002	0.027 \pm 0.001
	0.022 \pm 0.002	0.007 \pm 0.001	0.038 \pm 0.004	0.083 \pm 0.003	0.026 \pm 0.002
Lactating Female (N=71/28)	0.030 \pm 0.002	0.023 \pm 0.003	0.023 \pm 0.001	0.074 \pm 0.002	0.028 \pm 0.001
	0.022 \pm 0.003	0.006 \pm 0.001	0.039 \pm 0.004	0.082 \pm 0.003	0.028 \pm 0.003

Table 2.5 The average proportional nutrient intake per feeding bout, in absolute terms (grams),

± the standard error for all subsets during summer (top value) and autumn (bottom value). N

is the number of feeding bouts observed for each subset during summer (top) and autumn

(bottom). NSC=non-structural carbohydrates, NDF=neutral detergent fibre, AL=acid lignin.

	Crude Protein	Lipids	NSC	NDF	AL
Juvenile (N=162/48)	0.162 ± 0.006	0.123 ± 0.009	0.130 ± 0.003	0.425 ± 0.007	0.160 ± 0.004
	0.137 ± 0.010	0.040 ± 0.005	0.239 ± 0.019	0.443 ± 0.012	0.141 ± 0.009
Adults (N=204/94)	0.172 ± 0.006	0.131 ± 0.009	0.131 ± 0.002	0.412 ± 0.006	0.154 ± 0.004
	0.124 ± 0.008	0.039 ± 0.003	0.230 ± 0.014	0.464 ± 0.010	0.144 ± 0.007
Adult Females (N=133/58)	0.175 ± 0.007	0.127 ± 0.011	0.129 ± 0.003	0.414 ± 0.008	0.154 ± 0.004
	0.125 ± 0.010	0.038 ± 0.003	0.217 ± 0.015	0.467 ± 0.012	0.153 ± 0.010
Adult Males (N=71/36)	0.166 ± 0.010	0.140 ± 0.015	0.134 ± 0.004	0.406 ± 0.010	0.153 ± 0.007
	0.121 ± 0.013	0.041 ± 0.006	0.249 ± 0.025	0.460 ± 0.017	0.129 ± 0.012
Non-lactating Female (N=62/30)	0.183 ± 0.011	0.125 ± 0.016	0.130 ± 0.003	0.411 ± 0.011	0.151 ± 0.005
	0.126 ± 0.014	0.041 ± 0.005	0.213 ± 0.021	0.470 ± 0.018	0.149 ± 0.011
Lactating Female (N=71/28)	0.168 ± 0.009	0.128 ± 0.015	0.128 ± 0.004	0.418 ± 0.010	0.158 ± 0.006
	0.124 ± 0.015	0.035 ± 0.005	0.221 ± 0.023	0.463 ± 0.017	0.156 ± 0.016

During autumn, PERMANOVA detected significantly greater proportional intakes of all tested nutrients by females (n=58) compared with males (n=36) (CP: Pseudo-F=10.018; df=93; P=0.002; Lipids: Pseudo-F=6.4308; df=93; P=0.014; NSC: Pseudo-F=5.9004; df=93; P=0.018; NDF: Pseudo-F=95.972; df=93; P=0.001; lignin: Pseudo-F=18.429; df=93;

P=0.001). When tested with GLM, however, a significantly greater proportional consumption by female monkeys was only detected for NDF (P=0.000) and AL (P=0.001) with the proportional consumption of CP approaching significance (P=0.052). The proportional consumption of lipids (P=0.542) and NSC (P=0.396) were not detected with this statistical method. The average proportional amount consumed per feeding bout for males and females (per Kg of metabolic body mass) are presented in table 2.4 while the average amounts consumed in absolute terms are presented in table 2.5.

2.4.6 Nutrient Intake of Non-Lactating Females vs. Lactating Females

The proportional contribution of analysed nutrients to the diets of lactating (n=71) and non-lactating females (n=62) did not differ during summer: PERMANOVA: ((CP: Pseudo-F=.79711; df=132; P=0.361; Lipids: Pseudo-F=3.2861E⁻²; df=132; P=0.855; NSC: Pseudo-F=.33717; df=132; P=0.559; NDF: Pseudo-F=.22973; df=132; P=0.652; lignin: Pseudo-F=.23839; df=132; P=0.639)); GLM: (CP (P=0.942), lipids (P=1.000), NSC (P=0.999), NDF (P=0.998), and lignin (P=0.967)). The same trends were found in autumn (lactating females: n=28; non-lactating females: n=30): PERMANOVA: ((CP: Pseudo-F=2.374E⁻²; df=57; P=0.877; Lipids: Pseudo-F=.98017; df=57; P=0.32; NSC: Pseudo-F=7.496E⁻²; df=57; P=0.778; NDF: Pseudo-F=6.8435E⁻²; df=57; P=0.807; lignin: Pseudo-F=1.2902E⁻³; df=57; P=0.968)); GLM: (CP (P=1.000), lipids (P=0.975), NSC (P=1.000), NDF (P=1.000), and lignin (P=0.999)). The average proportional amount consumed per feeding bout for lactating and non-

lactating females (per Kg of metabolic body mass) are presented in table 2.4 while the average amounts consumed in absolute terms are presented in table 2.5.

2.5 Discussion

This study documents the seasonal foraging patterns and nutrient intake of a golden snub-nosed monkey troop in the Qinling Mountains and is the first study to investigate the effect of age, sex, and reproductive status on nutrient intake in this species. Documentation of their summer and autumn foraging illustrates what food types and species are important to this troop's diet. This has implications for the management of their habitat as critical resources can be protected. Furthermore, the differences found in nutrient intake patterns between juveniles and adults and between males and females further our understanding of how these factors can affect colobine nutritional ecology.

This troop consumed many different plant species during the two seasons. However, majority of their diet consisted of a relatively small number of species. The leaves of *Morus alba* were clearly the most important food species for this troop during both summer and autumn. Other plant species that were important components of this troop's diet were *Cornus* sp (fruit), *Pinus massoniana* (seeds), *Lindera obtusiloba* (fruit), *Quercus aliena* (seeds), *Litsea rubescens* (fruit), *Crataegus cuneata* (fruit), and *Prunus armeniaca* (leaves). *M. alba* was also consumed by snub-nosed monkeys in Hubei Province (Liu et al. 2013) and a member of the genus was consumed by monkeys in the same area as the current study (Guo et al. 2007). The

plants were not amongst the main contributors to the troop's diet in these studies, however. In Hubei Province, *M. alba* only made up 1.4% of feeding records (Liu et al. 2013) while the troop only spent 0.4% of the time consuming *Morus sp.* in Zhouzhi National Nature Reserve (Guo et al. 2007). Both *Q. aliena* and *L. obtusiloba* appear in feeding records from other studies: Zhouzhi National Nature Reserve (both species) (Guo et al. 2007), Hubei Province (*L. obtusiloba*) (Li 2006; Liu et al. 2013), and Qingmuchuan Nature Reserve (*Q. aliena*) (Li et al. 2010). *L. obtusiloba* was the fourth contributor to the troop's diet while *Q. aliena* was the main contributor in the previous study in Zhouzhi National Nature Reserve (based on time spent feeding) (Guo et al. 2007). While *L. obtusiloba* was a main dietary component for the troop in Hubei Province (12.2% of feeding records), *Q. aliena* was not consumed (Liu et al. 2013). Members of the *Cornus* genus were consumed by this species in multiple areas as well: Zhouzhi National Nature Reserve (Guo et al. 2007), Hubei Province (Li 2006; Liu et al. 2013), and Qingmuchuan Nature Reserve (Li et al. 2010). The troop in my study did not consume *Populus purdomii*, one of the main dietary contributors from the previous study in this reserve (Guo et al. 2007). Furthermore, the two main dietary contributors of the troop in Hubei Province, lichens and *Pinus armandii* (Liu et al. 2013), were not consumed in the current study. There is thus some overlap in plant usage across these studies but also some key differences. These disparities could be due to spatial and temporal variation in the occurrence of these plant species. Differences between these studies could also reflect differences in data analysis. My

results are based upon the number of grams consumed while the studies by Guo *et al.* (2007) and Liu *et al.* (2013) are based upon percentage of time feeding and proportion of feeding records, respectively. Although results based upon amount eaten and time spent feeding upon plant structural parts are comparable, fruit consumption can be underestimated using time based data compared with weight based data (Kurland & Gaulin 1987). It is thus unlikely that this error would be introduced when comparing *M. alba* consumption as leaves were consumed. The potential for this error should be considered for comparisons of other species for which fruit and seeds were consumed, however.

The relative availability of different food species is not a strong determinant in the food choice of this population of golden snub-nosed monkeys. Although a statistically significant result was only detected during autumn if the outliers were included, correlations between food choice and availability were negative both with and without outlier exclusion, supporting my prediction that this troop does not choose foods based on availability. Similar trends between food choice and availability have been found in other species. For example, Nilgiri langurs' (*Presbytis johnii*) (Oates et al. 1980) and François' langurs' (*Trachypithecus francoisi*) (Zhou et al. 2006) main dietary components did not include the most abundant plants in their habitat. Not all studies found this relationship between food choice and availability, however. Food abundance, as opposed to nutrient content, appears to be a stronger influence on Masked titi monkey (*Callicebus personatus melanochir*) food choice (Heiduck 1997).

There are other factors which can affect animal foraging behaviour besides food availability, however. For example, predator avoidance can influence food choice as larger trees may be safer places to feed, as opposed to on the ground or in small trees which may leave animals more vulnerable (Li et al. 2002). Data on golden snub-nosed monkey predation in the Qinling Mountains are minimal, unfortunately. Besides from one observation of a juvenile monkey taken by a goshawk (*Accipiter gentilis*), most reports are based upon observations of predators consuming dead monkeys (Zhang et al. 1999). If this troop was under strong predatory pressures, however, greater selection for larger trees upon which to feed would be expected. As tree size contributed to the availability index, this would have resulted in a positive relationship between food choice and availability if there was enough of an influence. Predation pressure may thus be weak in the Qinling Mountains (Kirkpatrick & Grueter 2010; Zhang et al. 2006a) and may explain why these monkeys travel and feed on the ground in addition to in the canopy (pers. obs.). Future studies on this troop's predation pressure would broaden our understanding of these monkeys' ecology and are recommended. Another influential factor in animal foraging is foods' nutritional content. Studies on the nutrient intake of other species suggest that animals aim to ingest a certain balance of nutrients (Johnson et al. 2013) or, when ecologically constrained from doing so, a certain amount of a prioritized nutrient (Felton et al. 2009b). These studies demonstrate that, instead of availability, specific

nutrient goals of animals determine their dietary intake. It is possible that food choice in the golden snub-nosed monkeys in our study is also likely to be driven by nutrient requirements.

Juveniles, adult males, lactating, and non-lactating females all showed a similar trend in seasonal plant part consumption in that fruit consumption decreased from summer to autumn while bark and seed consumption increased during that time frame. None of the differences in plant part consumption reached statistical significance, however. Other studies on the seasonal consumption of plant parts by primates typically find seasonal differences. For example, Japanese macaques (*M. fuscata yakui*) fed predominantly upon leaves in late winter/spring, fruit in summer and December, and seeds in autumn (Hill 1997). A golden snub-nosed monkey population in Hubei province also exhibited seasonal use of different plant parts. The troop mainly fed upon leaves April to September, fruits from June to October, seeds from September to March, and flowers from March to April (Liu et al. 2013). A previous study on golden snub-nosed monkeys in the Qinling Mountains found their summer diet to be mainly composed of leaves and seeds while their autumn diet was mainly composed of seeds and lichen (Guo et al. 2007). Statistical tests were not performed in these previous studies, however. It is thus not known if the seasonal differences described in these studies failed to reach statistical significance as in my study. It is possible that significant differences were not detected due to that fact that autumn observations took place early in that season. *Morus alba* leaves, the main contributor to this troop's diet, were still available during this time as were some fruits (e.g.

Celastrus orbiculatus, *Malus baccata*). Perhaps significant differences are detectable later in autumn with more pronounced phenological changes and hence differences in food type availability between the seasons. Future studies would benefit from exploring the full seasonality endured by these monkeys by including observations during late autumn/winter and spring.

When foods that made up at least 5% of the troop's diet (by weight) are considered to be main dietary contributors and are compared with remaining foods, no similarities in the balance of crude protein (CP), non-protein (NSC and lipids), and NDF were found amongst these main foods. This suggests that the troop is not focusing on foods that share characteristics with respect to the balance of these specific nutrients. Macronutrients and fibre are not the only factors that are important to animal nutrition, however (e.g. Milton 1999). Future studies on factors such as the vitamin, mineral, and energy content of their foods should thus be undertaken as these may reveal dietary patterns. Although main dietary foods did not share characteristics in terms of nutrient balance, majority of these foods lied on the outside of the area in nutrient space occupied by remaining foods. As such, most of these main dietary components lied at an extreme for single nutrients, containing a greater or smaller proportion of a nutrient than the rest of their diet. For example, during summer, one main food item had a smaller proportional CP contribution than remaining foods while 2 food items had a greater CP proportional contribution than remaining foods. It is purely speculative at this point but one

possibility is that the main foods of their diet are chosen for a factor not considered in my study (e.g. vitamins and/or minerals) and because, when consumed together, they balance out in terms of macronutrients and/or fibre as the foods are a mix of large and small proportional contributions. Further research into vitamin and mineral intake and how such intake relates interacts with macronutrient intake is clearly required.

The macronutrient composition of food items consumed by our focal troop varied seasonally with a reduction in proportional contribution of crude protein and lipids and an increase in non-structural carbohydrates' (NSC) contribution in autumn. The proportional contribution of NDF and lignin did not vary between the seasons. On average, seeds and bark were the main NSC, NDF, and lignin contributors to the troop's diet and leaves were the main CP contributors (see Appendix 1, Table A1.1). Fruits consumed by this troop were the greatest lipid contributors to their diet (see Appendix 1, Table A1.1). Fruit lipid concentrations are variable and high levels have been noted in other studies. The average proportional lipid contribution the fruits in my study is $12.57\% \pm 3.49\%$. The average lipid content of fruits consumed by golden snub-nosed monkeys in Hubei Province was 18.91% (Liu et al. 2013). Similarly, fruit lipid concentrations consumed by Panamanian primates averaged $11.8\% \pm 16.5\%$ (Milton 2008).

The proportional nutrient intake per bout coincided with seasonal changes in crude protein, lipid, and NSC in the food items. The high levels of lipids in this troop's fruits coupled

with the decline in fruit consumption in autumn likely explains the decrease in lipid contribution to the troop's diet. Similarly, the increase in seed and bark consumption likely lead to the observed increase in NSC consumption in autumn. The decrease in CP consumption in autumn despite the lack of a notable decrease in leaf consumption (with leaves being the main CP contributor to their diet) may also be explained by the decrease in fruit consumption as fruits were the second CP contributor to the troop's diet. Furthermore, bark and seeds, both of which increased in their diet in autumn, were relatively low in proportional CP content. NDF and lignin proportional intake patterns did not reflect the seasonal availability of these nutrients, however. Although lignin availability did not change, its proportional contribution decreased in autumn. Similarly, the proportional contribution of NDF in the foods did not change across seasons yet there was an increase in its proportional contribution to the troop's diet in autumn.

How the seasonal changes in proportional macronutrient consumption affect these monkeys biologically remains to be determined. The decrease in proportional CP and lipid consumption in autumn may seem counterintuitive as that is when females conceive. For humans, foetal growth appears to be more dependent upon the mother's nutritional status at the time of conception and in early pregnancy as opposed to her status later in pregnancy (Caan et al. 1987). The increase in proportional NDF consumption may help these monkeys cope with the decrease in CP availability in their foods, however, enabling them to maintain required CP

levels during this time (see below). The increase in proportional NSC consumption in autumn may be another way for these monkeys to cope with the decrease in CP and lipid availability. Autumn is also the time of the year when food sources begin to decline and the monkeys switch to a diet heavy in lichens (Guo et al. 2007). Lichens consumed by golden snub-nosed monkeys in Hubei Province generally contained less protein and fibre and more water soluble carbohydrates than other foods while lipid content was similar to some foods and lower than others (Liu et al. 2013). Whether lichens are an adequate food source for this troop in the Qinling Mountains remains to be determined. Quantifying the nutritional content of the lichens consumed by these monkeys and comparing those values with other known foods of the troop will help determine whether these monkeys undergo a period of nutritional stress during winter and whether they prepare for this during summer and autumn.

The increase in NDF's proportional contribution to their diet despite the nutrient not increasing in their food items during autumn may possibly be a way for these monkeys to cope with the decrease in the proportion of crude protein and lipids in their foods. Colobine monkeys are foregut fermenters and thus have a foregut containing microorganisms which break down the cell wall component of their foods (Edwards & Ullrey 1999). The fermentation of plant cellular walls results in the production of short chain volatile fatty acids (VFA) (Bauchop & Martucci 1968) which are an available energetic source for the monkeys. The energy provided through structural carbohydrate fermentation may make up for the loss of energetically rich

lipids during autumn. Although VFA are also made available through the fermentation of non-structural carbohydrates in ruminants (Moran 2005), it has been suggested that sugars are not efficiently fermented in colobines (Cork 1996) and that digestible foods bypass fermentation in the complex colobine stomach (Cork 1996). In such a case, sugars would avoid fermentation and would be digested by the monkeys. Bacterial fermentation of protein, which leads to the construction of microbial protein, supplies ruminants with notable amounts of the nutrient when the bacteria are digested (Agricultural and Food Research Council 1992). If it is the same with snub-nosed monkeys and their fermenting microorganisms, the monkeys would also acquire protein in such a manner. Lipids are not fermentable in ruminants (Agricultural and Food Research Council 1992) but it remains to be determined if this is also the case in colobines. The decrease in the proportional contribution of lignin to their autumn diet may also play a part in the strategy to use NDF as a source of VFAs and protein as the digestibility of cellulose and hemicellulose are both negatively impacted by lignin (Sullivan 1966). Thus, consuming foods that are lower in lignin would likely increase their digestive efficiency during these times of lower crude protein and lipid food content. As autumn is when females conceive and when juveniles are typically weaned (Qi et al. 2008), an increase in protein intake via increased proportional NDF consumption during this time would be expected.

No differences in plant species consumption patterns were detected between this population's subsets. On many occasions, the troop ate in very large trees that supported

multiple individuals meaning that individuals differing in age and sex fed upon the same tree, and hence species, together. A study on black howler monkeys (*Alouatta pigra*) in Mexico detected differences in plant species consumed between monkeys based on age and sex when analyses were based upon grams consumed but not when based on proportional data (Amato et al. 2014). Therefore, it is possible that the methods used in this study could not detect such differences and that further research is required to fully explore this aspect of this species' foraging behaviour.

Plant part consumption did not differ between this troop's subsets. Tufted capuchins (*Cebus nigritus*) demonstrated sex but not age related differences in the consumption of different food types with males consuming more animal matter and females consuming more fruit (Agostini & Visalberghi 2005). Sex-based differences in food type consumption has also been described in white-faced capuchins (*C. capucinus*). Females consumed smaller invertebrates and males consumed large invertebrates and vertebrates with sexual dimorphism proposed as a likely explanation (Rose 1994). Golden snub-nosed monkeys are also notably dimorphic yet did not demonstrate sex-based differences in feeding. One possible explanation for the differences in these results is that capuchins are more generalized in their diet (Fedigan 1990; Izawa 1978; Ottoni & Mannu 2001; Rose 1994) compared to snub-nosed monkeys. Perhaps this allows for greater dietary separation between capuchin conspecifics. Another possibility is that the methodology used in this study was not sensitive enough to detect the

differences. Not all differences were detectable in a study on black howler monkeys (*A. pigra*) if proportional data, as used here, were used (Amato et al. 2014). Analyses based upon weight consumed instead of proportion of observations were more revealing of differences in food consumption between conspecifics (Amato et al. 2014). Further studies on the foraging patterns of snub-nosed monkeys based on age, sex, or reproductive status using more sensitive methodologies are thus recommended.

Juveniles had a significantly greater proportional contribution of crude protein, NSC, lipids, NDF and lignin per Kg of metabolic body mass than adults during both summer and autumn as detected by both PERMANOVA and GLM. Differences in protein intake between juvenile and adult males were also detected in black howler monkeys (*A. pigra*) (Amato et al. 2014). Similarly, juvenile mountain gorillas (*G. beringei*) consumed more protein per Kg of metabolic body mass than adult males (Rothman et al. 2008b), while consuming the same non-protein to protein ratio as males (Rothman et al. 2011b). Such differences are likely due to the nutritional demands of growth and development of juveniles exceeding the demands of maintenance in adults. Furthermore, the fitness cost of malnutrition is high in juveniles. Protein-calorie malnutrition (PCM) in young rhesus macaques (*M. mulatta*), for example, can lead to weight loss, hair loss, muscular wasting, and pancreatic damage (Chopra et al. 1987; Racela Jr et al. 1966).

Females had a greater proportional contribution of crude protein, NSC, NDF, and lignin per Kg of metabolic body mass than males during summer and of all analysed nutrients during autumn when analysed using PERMANOVA. When analysed using GLM, the same results were obtained during summer but there were a few differences during autumn. There was a trend of a greater proportional intake of CP by females although it did not reach significance ($P=0.052$) as occurred in summer. A significant difference in the proportional consumption of NSC and NDF was not detected using GLM whereas a difference was detected by PERMANOVA. This suggests that PERMANOVA may be a more sensitive statistical test than GLM and was thus able to detect a smaller difference. Sex effects on nutrient intake have been recorded in other species. Female mountain gorillas (*G. beringei*) consumed more food and protein per unit of metabolic body mass than males (Rothman et al. 2008b). Similarly, female black howler monkeys (*A. pigra*) consumed more protein and energy per unit of metabolic body mass than males (Amato et al. 2014). The differences in nutrient intake patterns detected between the sexes in these species are likely due to the increased energetic demands of females due to factors such as pregnancy, lactation, and infant carrying (Clutton-Brock et al. 1989; National Research Council 2003; Picciano 2003; Tobey et al. 2006). The lack differences in the intake of all nutrients, or differences large enough to be detected, can potentially be due to the notable sexual dimorphism in this species. In highly dimorphic species, energy

expenditures between the sexes may balance out due to males having the increased costs associated with the maintenance of a large body (Key & Ross 1999).

No differences were detected in the proportional contribution of nutrients between lactating and non-lactating females, despite the prediction that lactating females would have greater energetic requirements. The results were same using both PERMANOVA and GLM. It is possible the sample size of our study and the methods we used for collecting data in the wild were not sensitive enough to detect subtle differences. Alternatively, females might change their diet as a fixed strategy, in anticipation of reproduction, rather than as a homeostatic response to reproductive status (Raubenheimer et al. 2012). Further studies are needed to disentangle these possibilities.

The samples used in this study were dried at higher temperatures which may affect the values of extracted nutrients. Although this will not affect our study as all samples were re-dried at the same temperature, other studies should take this into account when comparing results. Furthermore, many samples had to be collected from more than just the specific plant upon which the monkeys fed and not all samples were collected on the day of feeding data collection (but all were collected during the relevant season). Although this was the best compromise for obtaining enough samples for nutrient analysis, the nutritional content of plants can differ between different individuals of the same species and across space and time (Chapman et al. 2003) and can even change over the span of a day (Carlson et al. 2013). Greater

differences between different individuals compared with differences between species have been noted but differences between species are generally greater than differences between individuals (Chapman et al. 2003). Therefore, errors resulting from such sampling methods should not greatly affect the general conclusions of this study.

Further limitations of this study include the use of average weights for the monkeys and the lack of non-food sampling. Although the standard error of the average body weights used in this study are relatively small, it should be noted that the average juvenile weight was obtained from only four individuals. As juvenile weights could be expected to vary widely due to the growth and development that occurs during this life stage, there was likely variation in juvenile food and nutrient intake per Kg of metabolic body mass that was not accounted for in this study. Although to a lesser degree, weight variation in adult females and adult males are also expected and, similarly, would not have been accounted for in these analyses. Furthermore, plants that the troop did not feed upon were not sampled for nutritional content. Having such nutritional data would have allowed for additional analyses to be conducted. For example, determining whether foods and non-foods differ in any nutritional characteristics, as done by Liu *et al.* (2013) in Hubei Province, would have been possible. Such analyses would broaden our understanding of this species' nutritional ecology. Despite these limitations, this study has made an initial investigation into the trends of food choice and nutrient intake in this endangered colobine monkey, contributing to our understanding of primate nutritional ecology.

Chapter 3: The Impacts of Food Provisioning on Nutrient Intake in the Golden Snub-nosed Monkey (*Rhinopithecus roxellana*)



Two adult female snub-nosed monkeys and a juvenile in Zhouzhi National Nature Reserve. Photo by Brigitte Kreigenhofer.

3.1 Abstract

When wild animals are subjected to supplementary feeding, their ability to reach their nutritional target may be impeded if the nutritional composition of provisioned foods are unbalanced and non-complementary. Such an effect is likely to be exacerbated if supplementary feeding is accompanied by range restriction which reduces the animal's access to natural foods. Through comparison of the food and nutrient intake of two golden snub-nosed monkey (*Rhinopithecus roxellana*) troops, a wild troop and a provisioned troop at a wildlife tourism centre, I investigated how provisioning alters the nutrient intake of these monkeys. The proportional contribution of crude protein, lipids, non-structural carbohydrates, neutral detergent fibre, and lignin to each troops' foods and dietary intake were compared during summer and autumn. The foods consumed by the provisioned monkeys had a greater proportion of non-structural carbohydrates and lipids and less neutral detergent fibre and lignin compared with the foods of the wild troop. The proportional crude protein content of the foods consumed by the two troops did not differ. The differences in provisioned and natural foods resulted in significant differences in the proportional nutrient composition of the ingested diet of the two troops. Compared to the wild troop, the provisioned monkeys had a higher proportional intake of non-structural carbohydrates and a lower proportion of crude protein, neutral detergent fibre and lignin during both seasons. The provisioned monkeys' diet had a lower proportion of lipids during summer and a higher proportion of lipids during autumn. The differences in the nutrient intake of provisioned monkeys compared to wild conspecifics

warrants further research into potential health implications. The possibility of a diet high in non-structural carbohydrates and low in protein leading to problems such as obesity and type 2 diabetes mellitus in golden snub-nosed monkeys, as occurs in other primates, is of concern.

3.2 Introduction

Animal development, growth, maintenance, fecundity, and survival depend upon one of life's most basic processes: food intake. The acquisition from foods of specific nutrients in balanced proportions has emerged in recent years as a pronounced motivator in animal food choice (Raubenheimer 2011; Simpson & Raubenheimer 2012). Nutritional balancing theory is a relatively new approach in studying the nutritional ecology of both wild (Felton et al. 2009c; Johnson et al. 2013; Rothman et al. 2011b) and domesticated animals (Hewson-Hughes et al. 2013; Hewson-Hughes et al. 2011). Two fundamental questions in nutritional balancing theory are whether and how animals select foods to balance their nutrient gain (i.e. whether they select an "intake target"), and how they respond in circumstances when available foods do not enable them to achieve their target. Specifically, when confined to imbalanced foods the animal faces a trade-off between over-ingesting some nutrients and under-ingesting others (the "rule of compromise"). In a recent study, target selection in the wild was demonstrated by a female chacma baboon (*Papio hamadryas usinus*) who, using food items of widely diverging macronutrient ratios, consumed a consistent protein energy to non-protein energy balance each day, for thirty days (Johnson et al. 2013). Field studies examining the rule of compromise, to

date confined to primates, have revealed a diversity of strategies. Peruvian spider monkeys (*Ateles chamek*) (Felton et al. 2009b) prioritize protein intake by consuming relatively constant amounts of protein while allowing fluctuations in their take of carbohydrates and lipids, the same response as is shown by humans (Gosby et al. 2013; Martinez-Cordero et al. 2012). Mountain gorillas (*Gorilla beringei*), in contrast, prioritise non-protein energy, while sifaka lemurs (*Propithecus diadema*) maintain nutrient balance at the cost of reduced overall calorie intake (Irwin et al. 2015).

An important factor that has the potential to impact substantially on the ability of wildlife to reach their nutritional goals is food provisioning by humans, which can dramatically alter an animal's nutritional landscape. Food provisioning to wild animals is often employed as a tool at wildlife tourism sites to increase the chances of wildlife viewing by visitors (Green & Higginbottom 2001; Orams 2002) and to accommodate tourists to be close to and have contact with the animals (Green & Higginbottom 2001; Newsome & Rodger 2013). Previous studies on the effects of food provisioning on wild animal populations have mainly focused on how such practices affect animal behaviour (Berman et al. 2007; Fitzpatrick et al. 2011; Hammerschlag et al. 2012; Hines 2011; Hsu et al. 2009), population density (Ozoga & Verme 1982; Smith 2001; Walpole 2001), and degree of pathogen infestation and infection (Knapp et al. 2013; Vignon et al. 2010). Relatively few studies have addressed the effects of provisioning on animal diet and nutrition, and none of which I am aware have specifically looked at the

impacts on dietary nutrient balance. Studies conducted on Northern Bahamian Rock Iguanas (*Cyclura cychlura*) found that provisioned animals, unlike non-provisioned conspecifics, consumed unnatural food items such as trash, non-native fruits, and sand (Hines 2011). Provisioned iguanas also had unique blood profiles with altered levels of uric acid, glucose, and micronutrients such as potassium and calcium compared with non-provisioned conspecifics (Knapp et al. 2013).

Food provisioning has the potential to benefit wild animals. For example, food provisioning was one of the tools used in a successful conservation program for the Mauritius Kestrel (*Falco punctatus*) (e.g. Jones et al. 1995). Provisioning can also have detrimental effects, however. For example, animals that are not on a natural diet, such as those in captivity, may be fed foods in greater quantity and foods that are nutritionally imbalanced. Excess food and foods greater in energy content than wild foods were the likely cause of high rates of obesity in captive ruffed lemurs (*Varecia variegata*) (Schwitzer & Kaumanns 2001). Alternatively, provisioned foods might attract animals away from a balanced diet, resulting in health problems, as is the case for processed foods and human obesity (Raubenheimer et al. 2015). It is thus necessary to determine if and how specific food provisioning practices affect the nutrient intake of animals and the implications for their wellbeing.

In addition to provisioning, range restriction of wild animals is sometimes used to achieve improved wildlife viewing by tourists (e.g. Berman et al. 2007, pers. obs.). Restricting

the range of animals limits their access to the full variety of natural food items, potentially limiting their ability to reach their nutrient target. These effects can be exacerbated if provisioned foods are not properly dispersed, allowing for monopolization of provisioned foods. Range restriction may also raise the level of aggression between the animals (Berman et al. 2007), which may affect the nutrient intake of some individuals.

As in many parts of the world, wildlife tourism has been developing in Asian countries. For example, seeing and interacting with Tibetan macaques (*Macaca thibetana*) are part of tourists' experiences at Mt Huangshan in China (Berman et al. 2007), Japanese macaques (*Macaca fuscata*) can be seen at Takasakiyama in Japan (Kurita et al. 2008), and Formosan macaques (*Macaca cyclopis*) are on view at Shou-Shan Nature Park in Taiwan (Hsu et al. 2009). Due to the popularity of primates in tourism, the nutritional implications of provisioning and range restriction need to be addressed in this taxon. Such information will help managers to be aware of the potential effects of provisioning on nutrient intake of wild animals so that appropriate adjustments can be made to avoid detrimental effects on the health and fitness of targeted animals. Furthermore, any negative consequences of improper management will have an even greater impact on species that are endangered, where managed animals may make up a large proportion of the remaining population.

The golden snub-nosed monkey (*Rhinopithecus roxellana*), an endangered colobine primate endemic to China (IUCN 2010), occupies broadleaf, conifer, and mixed

broadleaf/conifer forests in mountain ranges in central and north-western China at altitudes ranging from 1,500 to 3,300 m above sea level. Their natural diet consists of a wide range of plants and lichen (Guo et al. 2007; Li 2006; Li et al. 2010) and they also consume some animals (insects, arachnids, vertebrates) (Li et al. 2002; Zhao 2008, pers.obs.). The plant parts they consume contain a high proportion of water soluble carbohydrates (WSC) and a low proportion of fibre (Liu et al. 2013). They have large home ranges and long daily travel distances (Kirkpatrick & Grueter 2010) as well as seasonal movements that coincide with plant phenology. The combination of a diverse diet and daily and seasonal movements within a large home range enable them to acquire sufficient nutrients without degrading their habitat. As a dominance hierarchy exists both between and within family units, referred to as one male units (OMUs) (Li et al. 2005; Zhang et al. 2008b), competition and food resource monopolization occur in this species (Zhang et al. 2008b). As golden snub-nosed monkeys are targeted for wildlife tourism in at least two areas in China (Shennongjia (Hubei Province) and the Qinling Mountains (Shaanxi Province)), this is a good species to use in studies on the effects of food provisioning on nutrient intake. Through comparison of nutrient intake patterns of a provisioned snub-nosed monkey troop and that of a free-range troop in the Qinling Mountains, I addressed the following questions: 1) Does the nutrient composition of the food items available to the provisioned troop differ from that of the foods consumed by the wild troop? I predicted that foods consumed by the two troops differed in nutrient composition due to the

conventional foods offered to the provisioned troop. 2) Does the proportional nutrient composition of food intake in the provisioned troop reflect that of the wild troop? I predicted that the provisioned troop's proportional nutrient intake differed from that of the wild troop due to the provisioned troop's diet being heavily influenced by human caretakers.

3.3 Methods

3.3.1 Study Sites and Focal Snub-nosed Monkey Troops

This study was conducted at two sites: Da Ping Yu Nature Reserve (107°58'E, 33°40'N), located on the southern slope of the Qinling mountains (Shaanxi Province, China), and Zhouzhi National Nature Reserve (108°16'E, 33°48'N) on the northern slope of the Qinling Mountains (Shaanxi Province, China) (Figure 3.1). Da Ping Yu Nature Reserve is a wildlife tourism site which allows tourists to view animals such as the giant panda (*Ailuropoda melanoleuca*) and golden snub-nosed monkeys. The monkeys in this reserve live in a natural setting but are restricted to a specific area. They are herded into the viewing area every morning by staff and are encouraged back into the viewing area if they try to leave during the day. They are provided with provisioned food items at least three times a day, every day, and have limited access to natural food items in their restricted area. Provisioned foods are distributed throughout the viewing area on the ground, resulting in these monkeys spending more time on the ground than free roaming monkeys (although the wild monkeys observed in Zhouzhi National Nature Reserve sometimes fed and travelled on the ground (pers. obs.)). As these natural food items are depleted, the monkeys are moved to a different area of the reserve from

time to time. At the time of this study, there were between 7 and 8 OMUs (approximately 70 individuals) provisioned and range restricted for tourism purposes.

Zhouzhi National Nature Reserve, where data on the wild troop were collected, was established in 1985 covers 53,000 ha (Zhao & Li 2009). Deciduous broadleaf forest is found from 1,400 m to 2,200 m, mixed deciduous broadleaf and conifer forest from 2,200 m to 2,600 m, and above 2,600 m, it is exclusively conifer forests (Li et al. 2000). The troop observed for this study, the west ridge troop (WRT), is one of two troops inhabiting the area. There were an estimated 175 individuals in the WRT.

3.3.2 Focal Animal Identification

Feeding data and food samples were collected from the following subsets of the two focal groups:

Non-lactating females (NLF): females who are sexually mature but who were not lactating.

Sexual maturity was indicated by breast and nipple size and/or by engaging in sexual behaviour.

Lactating female (LF): females who are sexually mature and who are breast feeding an infant.



Figure 3.1 The location of the two study sites: Da Ping Yu Nature Reserve ($107^{\circ}58'E$, $33^{\circ}40'N$) and Zhouzhi National Nature Reserve ($108^{\circ}16'E$, $30^{\circ}50'N$).

Adult male (AM): males who are sexually mature as indicated by their size and the presence of granulomatous flanges on both corners of their upper lips.

Juvenile (J): individual who is weaned and thus feeding on solid foods but who is not yet sexually mature. Infants were not included in this study.

3.3.3 Feeding Data Collection

Data were collected at Da Ping Yu Nature Reserve during May and June 2012 (summer) and October and November 2011 (autumn) and consisted of approximately 17,108 minutes of

observations (10,897 minutes during summer, 6,211 minutes during autumn). Animals were observed from their first feeding which typically occurred between 08:30 and 09:30 until their last feed, typically in the 17:00 hour. Monkeys were observed from the visitor observation area or from a location within the troop from distances ranging from 2 to 10 metres.

Data were collected in Zhouzhi National Nature Reserve from June to August of 2011 (summer) and during October of 2012 (autumn). The troop was followed for approximately 6,251 minutes (4,511 minutes in summer, 1,740 minutes in autumn). Animals were typically followed and observed between 08:00 and 17:00 hours. There was some variation in the observational hours, however, as the troop could not always be located immediately in the morning or because of inclement weather. As this troop is well habituated to human presence, they can be observed from short distances (as close as a few meters or from the base of their feeding tree). Movement through the troop's feeding area was minimized to reduce disturbances, however, so some individuals were observed from greater distances.

For both troops, scans were conducted to collect feeding data with scans beginning with the first feeding individual that was spotted and continuing in a clockwise manner through the rest of the troop. During each scan, focal animal sampling (Altmann 1974) was used to collect data from a single individual for a maximum of 10 minutes or until he/she stopped eating for 30 seconds, left the feeding area, or changed to another activity (e.g. grooming, playing, sleeping). This 10-minute maximum time frame is defined as a 'feeding bout' and is the

sampling unit. During each observed feeding bout, the food item, the food species, and the number of food items consumed were recorded. Once the feeding bout ended, or the focal animal went out of view for more than 30 seconds, the scan continued until another feeding individual was spotted. To estimate the weight consumed of each food item (e.g. a leaf or a piece of fruit), representative samples of food items that were observed to be eaten were collected once the monkeys left the area and an average weight of each item was calculated. Samples of consumed plants and/or photographs of the plants were collected for identification purpose. Plants were identified with the assistance of Dang Gaodi, Guo Songtao, and Li Baoguo. For plants not identifiable, the local name is used.

3.3.4 Food Sample Collection

An average weight for each provisioned food item was determined by weighing multiple pieces of each food type. Provisioned foods included carrots, parsnips, peaches (pulp and pit were weighed and analysed separately), apples, bananas (pulp and skin were weighed and analysed separately), dried corn, and peanuts (seeds). For natural food items, once the monkeys were no longer consuming them and had vacated the food tree, samples were collected and weighed. Natural foods included leaves, stems, and bark in the provisioned monkeys and leaves, seeds, bark, fruit, and fungus in the wild monkeys. Approximately 400-500 grams were collected of each food item, whenever possible. When individual trees could not offer sufficient quantity, samples were collected from multiple plants in the area and pooled. Samples were dried in an oven at 60°C (a minimal amount was dried in a food

dehydrator) until reaching a stable weight and were kept in the dark in sealable plastic bags before nutrient analyses at Northwest University (Xi'an). Samples were then re-dried at 105°C prior to nutrient analyses. As the drying temperature is above the recommended temperature of ~55°C (Rothman et al. 2011a), the possibility of an overestimate of fibre and underestimate of soluble sugars should be considered. Although no bias should be introduced into our study as all samples were re-dried at the same temperature.

3.3.5 Nutrient Analyses

For nutrient analyses, samples were ground using a 1mm mill and were analysed in triplicate. For determination of the crude protein (CP) content of food items, total nitrogen was determined using the Kjeldahl procedure (using a BUCHI, K-360) and nitrogen values were multiplied by 6.25 to estimate the CP content (Maynard & Loosli 1969; van Soest 1994). A petroleum ether extract (FOSS ST310, Shanghai) was used to determine the crude lipid content of their food items (Conklin-Brittain et al. 2006). Neutral detergent fibre (NDF), acid detergent fibre (ADF), and lignin (L) content were determined sequentially using the ANKOM A2000i FiberAnalyzer. Samples were assayed for neutral detergent fibre with residual ash (with sodium sulfite and α -amylase), then for acid detergent fibre with residual ash, and finally for lignin (Van Soest et al. 1991; Rothman et al. 2008b). Water soluble carbohydrate content was determined using the Anthrone method while Fehling's solution and 1% hydrochloric acid hydrolysis were used to determine the starch content of their food items (Lawler et al. 2006). During statistical analysis, the starch and WSC content of the food items were combined and

referred to collectively as non-structural carbohydrates (NSC). All nutrient values used in analyses are percent dry matter.

3.3.6 Data Analysis

Because the feeding bouts varied in duration, comparison of nutrient intake patterns across the two troops was restricted to proportional nutrient intakes per bout, rather than absolute amounts which are clearly determined by bout duration. The following nutrients were analysed: crude protein (CP), lipids, non-structural carbohydrates (NSC), neutral detergent fibre (NDF), and lignin (L). For each food item, the proportional contribution that each nutrient contributed to the CP-lipid-NSC-NDF-L portion of the food item was calculated using the following formula:

$$PC_1 = \frac{PN_1}{\sum_{i=N_1}^5 (Pi)}$$

where PC_1 is the proportional contribution of nutrient 1, P = the proportional contribution of the nutrient of interest to the food item. This was calculated for all five nutrients. Permanova (Primer6) was used to analyse the proportional composition of all food items' nutrients between summer and autumn and between the two monkey troops. To calculate the protein energy and non-protein energy (lipids and non-structural carbohydrates) content of foods, the following conversion factors were multiplied by the nutrients' contribution to the foods: crude protein: 16.7 kJ, lipids: 37.7 kJ, non-structural carbohydrates: 16.7 kJ (National Research Council 1989).

For each feeding bout, the estimated metabolic body mass ($M^{.762}$) (Rothman et al. 2008b) of the consumer (based on age and gender) was taken into account as food and nutrient intake are greatly determined by an animal's size (Nagy 2005). The following weight estimates were used: adult female: 9.72 kg; adult male: 16.81 kg; juvenile: 5.85kg (S. Guo, personal communication). The proportional contribution of each nutrient per Kg of metabolic body mass was thus calculated using the following equation:

$$PC/M = PC_i/m^{.762}$$

where PC = the proportional contribution of nutrient i to the feeding bout and m = the estimated body mass of the individual.

Permanova (Permutational Multivariate Analysis of Variance) (PERMANOVA+; Primer6) was used to test for differences in the proportional nutrient composition of the troops' foods. Both PERMANOVA and General Linear Model (GLM) (IBM SPSS 22) were used to test for differences in the proportional nutrient intake patterns between two troops. The independence and similar distribution of observations are the only assumptions of PERMANOVA (Anderson 2001) while GLM has the following assumptions: the errors of observations and the independent variables are independent, constant covariance of dependent variables across cells, and a multivariate normal distribution of the errors across the dependent variables (although the method is robust to deviations from this assumption) (IBM SPSS 22). To specifically investigate the crude protein, non-protein (lipid and non-structural

carbohydrate), and NDF balance in the foods and dietary intake of the two troops, a right-angled mixture triangle was used to visualize the proportional intake per feeding bout and the proportional composition of each troop's foods of these nutrients. For all analyses conducted using Permanova, the Euclidean distance was used in production of the resemblance matrix and all data were square root transformed prior to production of the resemblance matrix.

3.4 Results

3.4.1 Natural and Provisioned Food Consumption by the Two Troops

The provisioned monkeys consumed nine provisioned food items and sixteen naturally occurring plant species across the two seasons (Table 3.1). Despite there being a larger number of naturally occurring plant species in their diet, the greatest proportion of their diet by weight came from provisioned foods (98% vs. 2% for natural foods). The wild troop, by comparison, consumed 46 species, all of which occurred naturally within their habitat (Table 3.1).

Table 3.1 The number and percentage of natural and provisioned foods consumed by wild and provisioned monkeys across summer and autumn and the percentage of the troops' diet (by weight) made up by each food type.

	# of Natural Foods (species)	% of diet (in grams)	# of Provisioned Foods	% of diet (in grams)
Wild	46	100%	0	0
Provisioned	15	2%	9	98%

3.4.2 Seasonal Trends in the Nutrient Composition of the Provisioned Troop's Foods

The summer (n=20) and autumn (n=11) foods of the provisioned troop did not differ in the proportional contribution of any measured nutrients: crude protein (pseudo-f=0.92, df=29, P=0.335), lipids (pseudo-f=8.30E⁻⁴, df=29, P=0.926), non-structural carbohydrates (pseudo-f=3.60E⁻², df=29, P=0.858), NDF (pseudo-f=6.85E⁻², df=29, P=0.789), lignin (pseudo-f=6.08E⁻², df=29, P=0.791) (Table 3.2).

Table 3.2 The average proportional contribution of nutrients to the provisioned troop's food during summer and autumn. CP=crude protein, NSC=non-structural carbohydrates, NDF=neutral detergent fibre.

	% CP	% Lipids	% NSC	% NDF	% Lignin
Summer (n=20)	0.135 ± 0.018	0.111 ± 0.032	0.281 ± 0.046	0.366 ± 0.040	0.107 ± 0.015
Autumn (n=11)	0.100 ± 0.015	0.090 ± 0.020	0.307 ± 0.072	0.391 ± 0.060	0.112 ± 0.018

3.4.3 Provisioned Troop Foods vs. Wild Troop Foods

Compared with foods consumed by the wild troop (n=66), the provisioned troop's foods (n=31) as a whole had a greater proportional contribution of lipids (pseudo-f=14.64, df=96, P=0.001) and non-structural carbohydrates (pseudo-f=9.10, df=96, P=0.002) and a smaller contribution of NDF (pseudo-f=16.15, df=96, P=0.002) and lignin (pseudo-f=9.15, df=96, P=0.003) (Table 3.3). Although not statistically significant, there was a trend of a lower contribution of crude protein to provisioned foods (pseudo-f=2.93, df=96, P=0.092) (Table 3.3). The proportional nutrient composition of all foods consumed, as well as the contribution

to the troops' diet (by weight), is in Appendix I, Table A1.3 (provisioned troop) and Appendix I, Table A1.1 (wild troop). The average non-protein energy to protein energy ratio of the foods consumed by the wild monkeys was 2.05 while that of the foods consumed by the provisioned troop was 4.40 (Figure 3.2).

Table 3.3 The average proportional nutrient content for foods consumed by the provisioned troop and wild troop across both seasons. CP=crude protein, NSC=non-structural carbohydrates, NDF=neutral detergent fibre. * = significant difference between the troops (P<0.05).

	% CP	% Lipids*	% NSC*	% NDF*	% Lignin*
Provisioned (n=31)	0.123 ± 0.013	0.104 ± 0.022	0.290 ± 0.038	0.375 ± 0.033	0.109 ± 0.012
Wild (n=66)	0.149 ± 0.010	0.047 ± 0.006	0.183 ± 0.009	0.466 ± 0.009	0.155 ± 0.009

3.4.4 Seasonal Trends in the Nutrient Composition of the Two Troops' Dietary Intake

Analyses using PERMANOVA suggest the provisioned troop's diet had a significantly greater proportional contribution of non-structural carbohydrates in both summer and autumn (Summer: pseudo-f=1697, df=1099, P=0.001; Autumn: pseudo-f=409.58, df=934, P=0.001) and a significantly lower proportion of NDF (Summer: pseudo-f=561.01, df=1099, P=0.001; Autumn: pseudo-f=391.82, df=934, P=0.001) and lignin (Summer: pseudo-f=1365.1, df=1099, P=0.001; Autumn: pseudo-f=325.34, df=934, P=0.001). There was also a lower proportional intake of crude protein by the provisioned group (Summer: pseudo-f=36.128, df=1099,

P=0.001; Autumn: pseudo-f=53.48, df=934, P=0.001). The provisioned group had significantly lower proportional intake of lipids during summer (pseudo-f=42.345, df=1099, P=0.001) compared to the wild troop but this trend was reversed in autumn when the provisioned troop had a significantly greater proportional intake of lipids (pseudo-f=192, df=934, P=0.001) (Fig.3). Analyses using GLM suggest the same results: summer (CP: F=38.200, df=1099, P=0.000; Lipids: F=66.038, df=1099, P=0.000; NSC: F=1218.010, df=1099, P=0.000; NDF: F=509.918, df=1099, P=0.000; Lignin: F=1137.035, df=1099, P=0.000) and autumn (CP: F=75.872, df=934, P=0.000; Lipids: F=103.889, df=934, P=0.000; NSC: F=330.422, df=934, P=0.000; NDF: F=351.433, df=934, P=0.000; Lignin: F=333.213, df=934, P=0.000). The average proportional nutrient intake per kg of metabolic body mass for each troop during summer and autumn are presented in table 3.4 while the average proportional nutrient intake on an absolute basis are presented in Table 3.5.

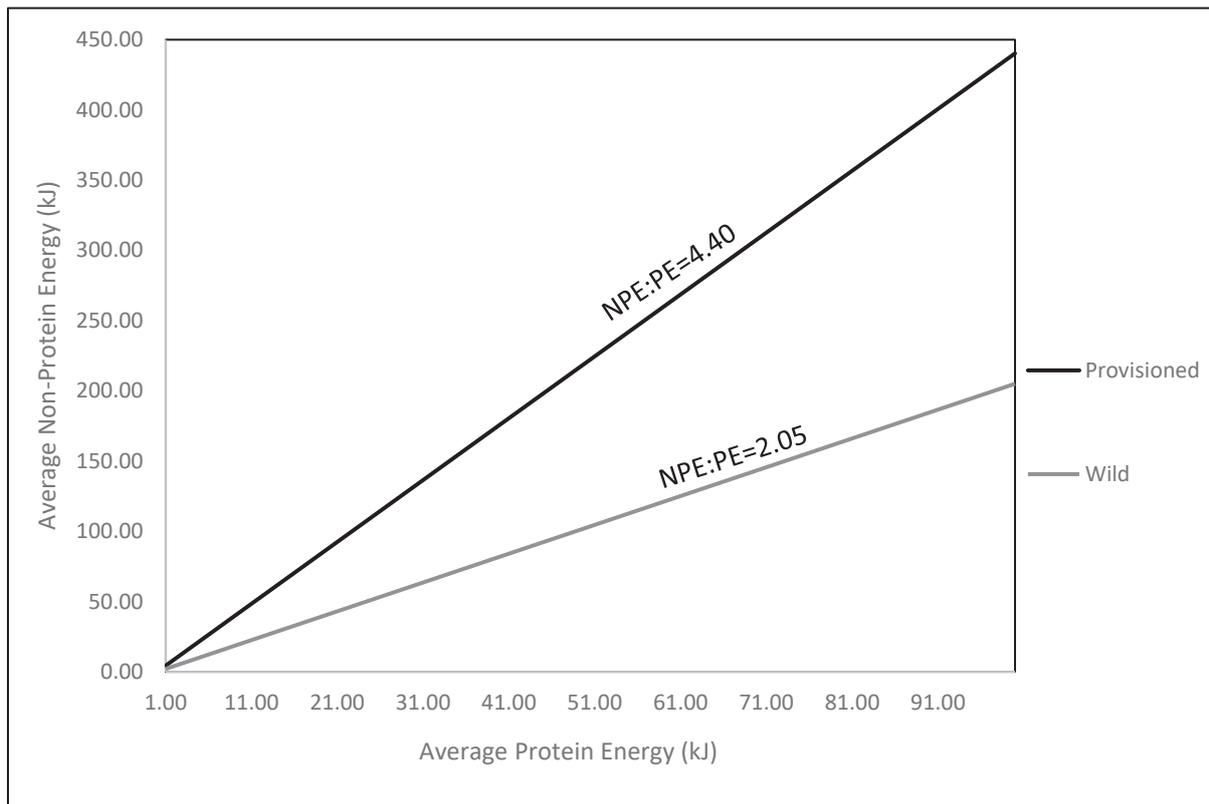


Figure 3.2 The average non-protein (lipids and non-structural carbohydrates) energy to protein energy ratio of foods consumed by the provisioned troop and wild troop.

Table 3.4 The average proportional nutrient intake per feeding bout (grams per kg of metabolic body mass) +/- the standard error for the wild and provisioned troops during summer and autumn. n is the number of feeding bouts observed for each troop during summer and autumn.

All intertroop differences are significant ($P < 0.05$).

Troop	Season	% CP	% Lipids	% NSC	% NDF	% AL
Wild	Summer (n=366)	0.034 ± 0.001	0.025 ± 0.001	0.026 ± 0.001	0.085 ± 0.002	0.032 ± 0.001
	Autumn (n=142)	0.025 ± 0.001	0.008 ± 0.001	0.044 ± 0.002	0.086 ± 0.002	0.027 ± 0.001
Provisioned	Summer (n=734)	0.027 ± 0.001	0.016 ± 0.000	0.090 ± 0.001	0.044 ± 0.001	0.009 ± 0.000
	Autumn (n=793)	0.016 ± 0.000	0.015 ± 0.000	0.115 ± 0.002	0.037 ± 0.001	0.010 ± 0.000

Table 3.5 The average absolute nutritional intake per feeding bout (grams) for the wild and provisioned troops during summer and autumn. n is the number of feeding bouts observed for each troop during summer and autumn.

Troop	Season	% CP	% Lipids	% NSC	% NDF	% AL
Wild	Summer (n=366)	0.168 ± 0.004	0.127 ± 0.006	0.131 ± 0.002	0.418 ± 0.005	0.157 ± 0.003
	Autumn (n=142)	0.128 ± 0.006	0.040 ± 0.003	0.233 ± 0.011	0.457 ± 0.008	0.143 ± 0.006
Provisioned	Summer (n=734)	0.145 ± 0.002	0.086 ± 0.002	0.488 ± 0.005	0.232 ± 0.004	0.049 ± 0.001
	Autumn (n=793)	0.080 ± 0.002	0.079 ± 0.001	0.604 ± 0.006	0.190 ± 0.004	0.048 ± 0.001

3.4.5 Crude Protein, Lipid and Non-structural Carbohydrate, and Neutral Detergent Fibre (NDF) Composition of the Two Troops' Foods and Dietary Intake

Testing the balance between the proportional crude protein, non-protein (lipid and non-structural carbohydrate), and NDF contribution to the troops' foods and dietary intake, foods consumed by the provisioned troop had significantly less crude protein (pseudo-f=4.95, df=1, P=0.031) and NDF (pseudo-f=17.98, df=1, P=0.001) and more lipids and non-structural carbohydrates (pseudo-f=17.11, df=1, P=0.001) than the foods of the wild troop (Figure 3.1). Similarly, the provisioned troop's proportional nutrient intake was significantly lower in crude protein (pseudo-f=217.85, df=1, P=0.001) and NDF (pseudo-f=1698.3, df=1, P=0.001) and higher in non-protein (pseudo-f=1611.9, df=1, P=0.001) than the wild troop (Figure 3.3).

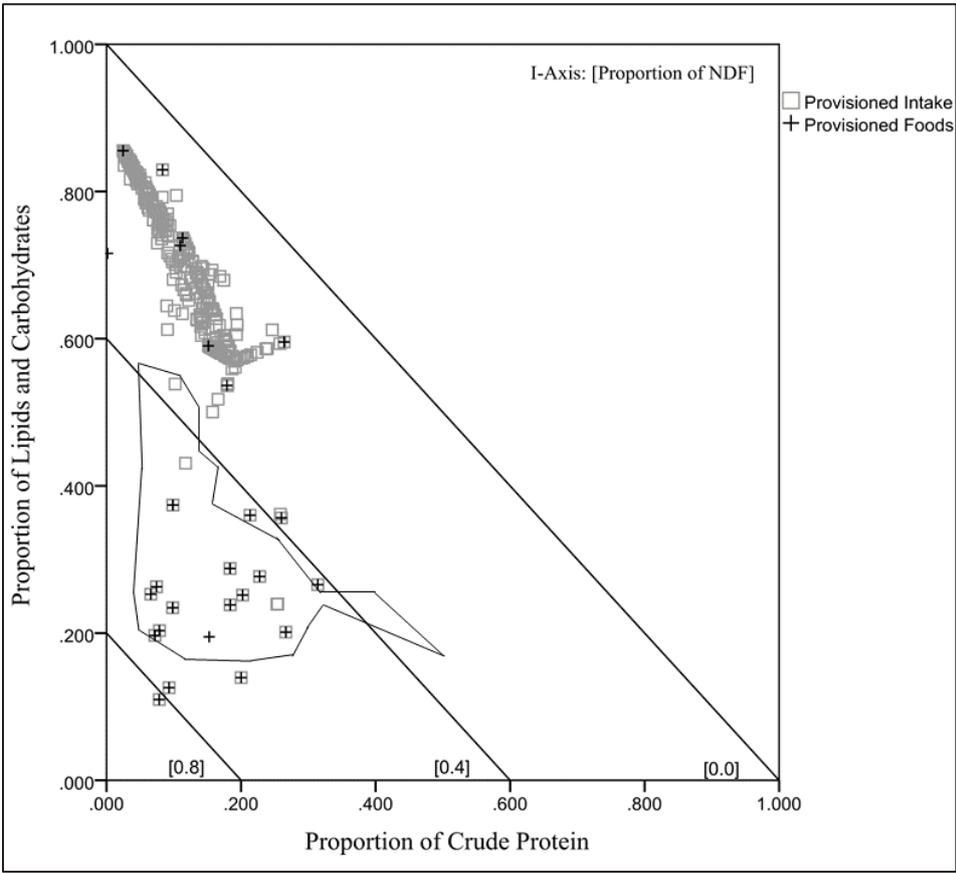
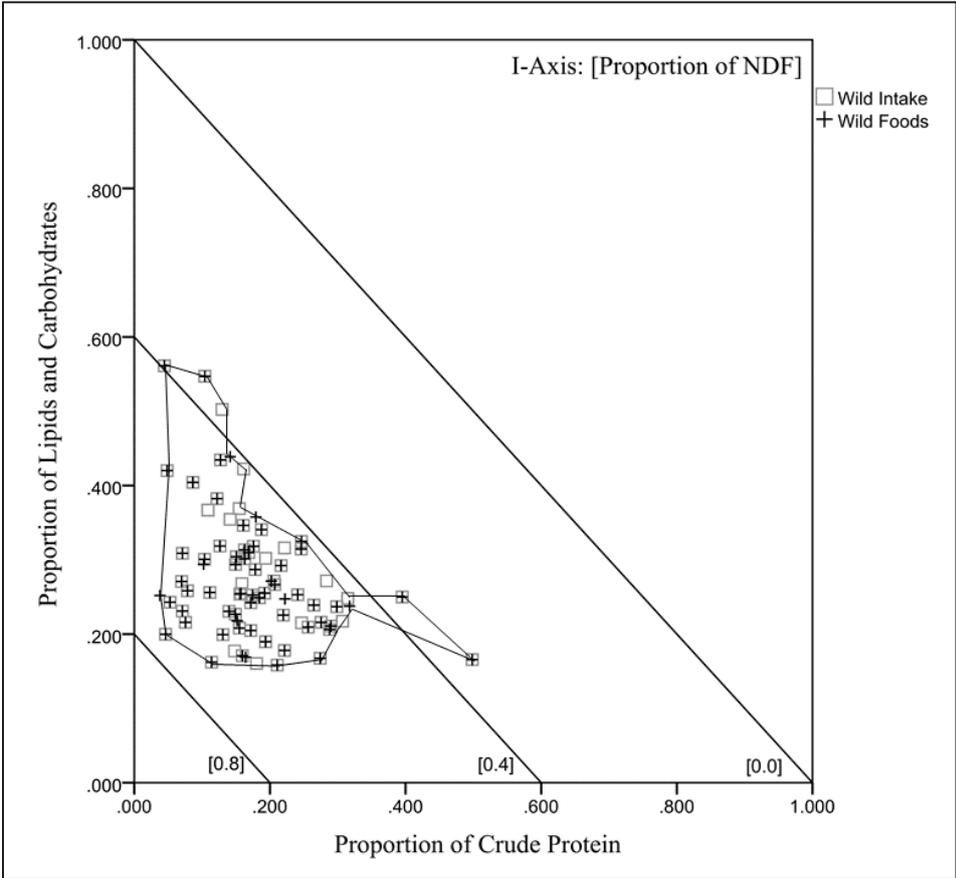


Figure 3.3 The crude protein, lipids and non-structural carbohydrate (non-protein), and NDF proportional contribution to the foods and nutrient intake of (a) the wild troop and (b) the provisioned troop. The black outline, drawn visually to connect the outermost points reached by the wild troop's foods and/or intake, is superimposed on that of the provisioned troop for comparison. As nutritional outliers are important as they may possibly be used to balance other foods, they were included in the outline. The provisioned foods contained proportionally more non-protein and less crude protein and NDF than wild foods (crude protein: pseudo-f=4.95, df=96, $p=0.031$; non-protein: pseudo-f=17.11, df=96, $p=0.001$; NDF pseudo-f=17.98, df=96, $p=0.001$). The nutritional intake of the provisioned troop contained proportionally more non-protein and less crude protein and NDF than that of the wild troop (crude protein: pseudo-f=217.85, df=2034, $p=0.001$; non-protein: pseudo-f=1611.9, df=2034, $p=0.001$; NDF: pseudo-f=1698.3, df=2034, $p=0.001$). The implicit axis, with values given in brackets, runs inverse to the x axis. The proportional NDF content is thus found by determining where the isoline passing through the relevant point intercepts the x-axis, and subtracting the x-value of that point from 1.

3.5 Discussion

This study is the first to investigate food and nutrient intake in a provisioned group of Colobine monkeys as compared to wild conspecifics. The results of this study suggest that the golden snub-nosed monkeys provisioned at Da Ping Yu Nature Reserve differ notably in their

food and nutrient intake compared with monkeys in Zhouzhi National Nature Reserve. This is the result of the differences in the nutrient compositions of provisioned foods with that of wild foods and the large proportion of the provisioned monkeys' diet made up of provisioned foods.

The provisioned troop's diet (by weight) was predominantly comprised of supplementary foods provided by humans. While natural foods were somewhat limited due to the monkeys being confined to specific areas (until natural foods were nearly depleted) and hence feeding upon a relatively small number of individual plants compared with free ranging monkeys, there may have also been sensory effects influencing their feeding behaviour. In other words, provisioned foods may have 'tasted better' than natural foods. Most food sensory studies on primates investigated thresholds for soluble sugars (Hladik & Simmen 1996; Laska 1996; Laska et al. 1998; Laska et al. 1999; Remis & Kerr 2002) and bitterness (e.g. Remis & Kerr 2002; Simmen & Hladik 1998). Previous research suggests a relation between soluble sugar sensitivity and body mass with larger primates becoming more sensitive to sugar (Hladik & Simmen 1996). Additionally, the likelihood of food selection being influenced by the sugar content, and hence sweetness, of foods has been suggested for various primates such as squirrel monkeys (*Saimiri sciureus*) (Laska 1996), baboons (*Papio hamadryas anubis*) (Laska et al. 1999), and western gorillas (*Gorilla gorilla gorilla*) (Remis & Kerr 2002). It is also possible, however, that snub-nosed monkey food selection is more heavily regulated by post-ingestive effects as has been suggested for leaf eating monkeys in general (Hladik & Simmen 1996).

Whether sweetness and/or post-ingestive effects influence food choice in snub-nosed monkeys, and the implications this has for food provisioning in this species, remains to be determined.

The foods consumed by this troop did not differ in proportional nutrient composition between summer and autumn. When compared with foods consumed by the wild troop, however, there were significant differences in the proportional contribution of nearly all tested nutrients. The foods of the provisioned troop had a greater proportion of lipids and non-structural carbohydrates and a lower proportion of NDF and lignin compared to that of the wild troop. The proportional crude protein content was lower in the provisioned foods with the difference approaching significance. The differences in the nutrient makeup of food items of the two troops have resulted in differences in the nutrient intake patterns between the provisioned and wild troops. The provisioned monkeys' diet contains a higher proportion of non-structural carbohydrates and less crude protein, NDF and lignin compared to the wild troop's diet. The lipid component of the provisioned diet varied from lower in summer to higher in autumn compared with the wild monkey's diet. Similarly, differences in the proportional contribution of crude protein, non-protein, and NDF to the troops' foods resulted in differences in the proportional intake of these nutrients by the two troops.

The nutrient intake target of this species remains to be determined as well as the nutrient they prioritize when unable to reach their target. Determining these in wild animals can be difficult, especially for those species inhabiting areas of harsh terrain and who live in large

groups as these factors impede the ability of researchers to obtain robust data sets based on full day focal animal sampling. Furthermore, experimentally confirming nutrient target results through feeding trials would be challenging with wild animals. Although such data are lacking for this species, trends in food nutrient intake, which are nevertheless revealing, were gathered here. The disparity in the proportional nutrient composition of the diets of these two troops is of concern and warrants further research. Similar shifts in the nutrient composition of foods consumed in current day Western human cultures, specifically the decrease in the protein to non-protein energy ratio, are theorized to be associated with the notable rise in human obesity (Gosby et al. 2013; Popkin et al. 2012). Furthermore, protein and fibre are both associated with satiation in humans (Fizman & Varela 2013), promoting appetite control. High protein levels are also important for fibre fermentation in ruminants (Putnam et al. 1966) and this may also possibly be the case with colobine monkeys, who also have fibre fermenting capabilities. Further investigation is required to determine whether the low crude protein and fibre composition of the provisioned group's diet leads to weight gain and its associated medical complications as well as decreased fibre fermentation.

Additionally, investigating the effects of a relatively high non-structural carbohydrate diet on their health is of interest for multiple reasons. Firstly, the fermentation efficiency of ruminants decreases while on a high sugar diet due to sugar induced acidosis in the forestomach (Van Soest 1982). The same may occur in other foregut fermenters such as colobine monkeys.

Secondly, high sugar diets have the potential to impact dental health, commonly leading to dental caries (Johnson-Delaney 2008). Thirdly, as high sugar diets are linked with conditions such as type II diabetes mellitus (T2DM), determining the susceptibility of golden snub-nosed monkeys to T2DM when on a high sugar diet would be of interest. As with humans, rhesus macaques (*M. mulatta*) are susceptible to diet-induced metabolic syndrome and T2DM (Bremer et al. 2011). Woolly monkeys (*Lagothrix lagotricha*) are also susceptible to diabetes (Vermeer 1994). Knowing the point at which such conditions manifest themselves in species under the care of humans, such as these golden snub-nosed monkeys, is important in terms of their management and wellbeing.

As a general guideline for primates in captivity and hence not on a completely natural diet, decreasing the amount of fruits and increasing the amount of vegetables in their diet is recommended (Clauss & Hatt 2011). Designing a diet following these guidelines and based on the nutrient intake data collected from wild snub-nosed monkeys is a good starting point for improving their diet in the absence of experimentally derived data on their nutritional target (e.g. Hewson-Hughes et al. 2013). The average non-protein energy (NPE) to crude protein energy (CPE) ratio of the foods consumed by wild golden snub-nosed monkeys during our study is 2.05. There are conventional fruits and vegetables with a NPE to CPE ratio not vastly different from the average ratio of their natural foods. These foods fall on either side of the ratio of their natural food average and could thus be complementary if offered together,

allowing the monkeys to reach a macronutrient ratio similar to that of wild conspecifics (Raubenheimer & Simpson 1997). These foods include: beetroot, bok choy, cabbage, carrots, celery, chard, corn, cucumber, lettuce, parsley, peanuts, and spinach. Carrots are already offered to the provisioned monkeys as are peanuts and corn. The provided corn is dried, however, which raises concern for the dental health of the monkeys (e.g. Cuzzo & Sauter 2006) – fresh corn may be preferable. Offering these foods may allow the provisioned monkeys to consume a more balanced diet, at least in terms of macronutrients. Micronutrients (vitamins and minerals) also need to be considered and should be included in diet design upon evaluation of their micronutrient consumption.

There may be financial and logistical (e.g. availability) constraints placed on wildlife tourism sites such as Da Ping Yu Nature Reserve, however, which may make such dietary changes difficult to implement. One way to work around the financial constraints of feeding a higher quality diet to provisioned animals would be to limit the number of animals kept on view. With fewer animals to feed, it may become feasible to offer a preferable diet. Therefore, I recommend a reduction in number of animals used for such tourism activities. Reducing the number of individuals used in tourism will also reduce the impact on wild populations, which is especially important for endangered species with small natural populations where each individual may be important genetically for the survival of the species.

Despite the potential risks involved for the focal animals, wildlife tourism can raise awareness and support for wildlife and their conservation (Xiang et al. 2011). Integrating current knowledge of animal nutrition to design nutritional balanced diets, reducing animal density, and reducing the degree of range restriction imposed on animals will minimize negative impacts on the animals while still enabling people to interact with nature. Collaboration between researchers and tourism managers will greatly benefit the industry by seeking sustainable wildlife tourism practices.

Similar to Chapter 2, there are limitations in this study which need to be considered. First, the samples used in this study were dried at higher temperatures than recommended which may have affected the values of extracted nutrients. All samples in this study were treated the same, however, so trends in my results should not be affected. This needs to be considered, however, if these data are to be used for comparative purposes in other studies. Second, many samples were collected from multiple plants of the same species and pooled. The possibility of individual variation in nutritional content (Chapman et al. 2003) needs to be considered. Third, average body weights were used as it was not possible to weigh every individual observed. The averages, while not having large standard errors, were obtained from a small number of individuals. This is particularly true for juveniles who are expected to have the greatest weight variation due to the amount of development that occurs in this age class. Fourth, non-food items were not analysed for nutritional content at either site. Determining the

differences between foods and non-foods would allow us to further understand the nutritional ecology of this species and is thus recommended for future research. Fifth, neither troop was sampled during all four seasons or during the same seasons across multiple years due to constraints. It is therefore not possible to account for seasonal differences during an entire year or for differences across years. Despite these limitations, this study provides insight into how food and nutrient intake trends can differ between naturally feeding and provisioned colobine monkeys. These results have implications for operations who utilize wildlife provisioning and will hopefully encourage the consideration of nutrition in the management of provisioned animals.

Chapter 4: Nutritional Ecology in a Captive Environment: the Effect of Age, Sex, and Social Status on Black-handed Spider Monkey (*Ateles geoffroyi*) Food and Nutrient Intake



The Auckland Zoo's spider monkey troop. Photo by Brigitte Kreigenhofer.

4.1 Abstract

The ability of animals to reach their nutritional goals is of utmost importance in terms of their fecundity, survival, and wellbeing. It is therefore imperative to understand animal food and nutrient intake patterns under various circumstances. Such information can be used to advance captive animal husbandry. The nutrient composition of foods offered to a captive black-handed spider monkey (*Ateles geoffroyi*) troop was analysed to determine the macronutrient space made available to the monkeys. Additionally, full day focal animal sampling was used to quantify the daily food and nutrient intake patterns of focal animals. Focal animals differing in age, sex, and social status were observed to reveal whether any of these factors affected their daily dietary intake. This captive troop is provided with a range of foods varying widely in macronutrient composition. Observations showed that focal animals selected foods to maintain a target macronutrient ratio, suggesting the offered diet was not constraining and that they did not have to make nutritional compromises. Juveniles consumed more food per kg of metabolic body mass than adults and geriatrics and consumed more of all tested nutrients per kg of metabolic body mass than adults. Juveniles consumed more of all nutrients, except for non-structural carbohydrates, than geriatrics. No differences in food or nutrient intake were detected between individuals based on sex or social status. These results demonstrate the feasibility of providing captive animals with a nutritionally balanced diet.

4.2 Introduction

As obtaining required nutrition is fundamental to animal health and welfare, the ability of animals to meet their nutritional requirements is of utmost importance for their fitness. Consequently, knowledge of wildlife nutrition is important for animal conservation and management, not only for wild populations, but also for animals that are under the care of humans. Such animals include those who are supplementary fed to assist in research (e.g. Yao et al. 2011), tourism (Newsome & Rodger 2013), or for management purposes (e.g. Schoech et al. 2008; Townsend et al. 1999), and those in captive environments who receive the majority if not all of their food from caretakers.

As animals in zoos and other captive environments depend on human designed diets, it is imperative that provided foods meet their nutritional requirements. This is important as improper diets can lead to undesirable results such as obesity (Schwitzer & Kaumanns 2001), which can then lead to further complications such as heart disease, diabetes, lethargy, and reproductive problems (Goodchild & Schwitzer 2008). In extreme cases, animals may die as a result of an inadequate diet. Such circumstances led to the death of five captive giraffes (*Giraffa camelopardalis*) who were unable to meet their energetic requirements during colder times of the year (Potter & Clauss 2005).

Studies using the nutritional balancing model, a comprehensive model which takes into account the interactions between multiple nutrients (Raubenheimer & Simpson 1997), have revealed that through food selection, animals seek to maintain a targeted macronutrient

balance. The optimal macronutrient ratio sought by animals varies across taxa (e.g. Felton et al. 2009b; Hewson-Hughes et al. 2013; Hewson-Hughes et al. 2011; Johnson et al. 2013; Rothman et al. 2011b). If an animal's desired nutrient intake cannot be realised due to the lack of balanced or complementary imbalanced foods, animals show a pattern of trade-off reflecting the relative priority assigned to the different nutrients. One such response is absolute prioritisation of a particular nutrient, in which the target level of that nutrient is ingested while the intake of other nutrients is allowed to fluctuate depending on the nutrient composition of available foods (Raubenheimer & Simpson 1997). Wild Peruvian spider monkeys (*Ateles chamek*) prioritise protein energy (Felton et al. 2009b) while mountain gorillas (*Gorilla beringei*) prioritise non-protein energy (Rothman et al. 2011b).

Nutrient intake patterns can also vary between members of the same species due to factors such as age and sex. For juveniles, this is likely due to the high cost of growth and development (National Research Council, 2003). Differences in nutrient intake between males and females (and between females) are expected to occur due to the costs associated with pregnancy, lactation, and child carrying (Clutton-Brock et al. 1989; National Research Council 2003; Picciano 2003; Strier 2000; Tobey et al. 2006). Differences in food (and hence nutrient) intake based on these factors have been noted in many primates (McCabe & Fedigan 2007; Murray et al. 2009; O'Mara & Hickey 2014; Rothman et al. 2008b). Social factors such as rank can also affect the nutrient intake patterns of animals. In wild wedge-capped capuchins (*Cebus*

nigrivittatus), the dominant female of the group prohibits group members other than her offspring and some juveniles from accessing fruit trees (Robinson 1981). Similarly, wild subordinate brown capuchins (*Cebus apella*) are denied access to favoured food sources, particularly fruit trees, due to aggression received from the dominant male (Janson 1990). Social status may thus have implications in captive environments as food may be controlled by dominant individuals. Investigation of such aspects in wild populations is challenging due to the difficulties of following individuals in the wild and obtaining accurate data on all food items they consume. Zoo populations, by contrast, are highly visible and fed controlled diets, making them good study subjects for research on factors influencing nutrient intake. The aims of this study are to investigate the nutrient composition of food items provided to captive black-handed spider monkeys in the Auckland Zoo and the nutrient composition of the selected daily diet. These data enabled us to evaluate whether the animals select a diet to maintain a stable dietary nutrient balance and how age, sex, and social status impact on nutrient intake.

Previous studies on spider monkey nutritional intake have been conducted on wild Peruvian spider monkeys (*A. chamek*), a sister species of the black-handed spider monkey from the same genus with an allopatric distribution (IUCN 2010). The daily ratio of non-protein energy (NPE) (carbohydrates and lipids) to available protein energy (APE) intake of wild Peruvian spider monkeys was 8:1 kcal (Felton et al. 2009b). When this could not be achieved, the monkeys prioritised protein intake (Felton et al. 2009b). These monkeys maintained a

relatively tight daily protein energy intake of 0.19 ± 0.01 mJ while they allowed their daily intake of carbohydrate and lipid energy to fluctuate widely (between 0.7 and 6.2 mJ), ultimately resulting in a variable daily energy intake (Felton et al. 2009b). The effects of age and social status on their nutrient intake have not been investigated, however.

Socially, wild black-handed spider monkeys typically segregate according to sex with males banding together into a group while travelling and foraging and females foraging in a more solitary manner, typically just with their offspring (Fedigan & Baxter 1984). Most aggression in the troop flows from males to adult females (Fedigan & Baxter 1984; Slater et al. 2009), usually during feeding or resting times (Fedigan & Baxter 1984). Females rarely direct aggression towards males and most female-female aggression occurs during feeding and is directed towards immigrants, suggesting the behaviour is rooted in competition (Asensio et al. 2008; Slater et al. 2009). Social factors are thus an important consideration in the food and nutrient intake patterns of spider monkeys.

In this study, the following questions were addressed: 1) Does the diet offered in the zoo constrain the monkeys from reaching a desired macronutrient balance? If their diet was constrained, I predicted that their daily macronutrient intake pattern would display nutrient prioritisation as opposed to ratio maintenance and that they would prioritise protein intake as was recorded in wild Peruvian spider monkeys, a closely related species. 2) Does the amount of food consumed per day differ between individuals of different age, sex, and social status? I

predicted that juveniles and high ranking animals would have a greater daily food intake per kg of metabolic body mass. As females are expected to have greater nutritional requirements due to pregnancy, lactation, and infant carrying, differences between the adult females and adult male in this study were not expected as none of the females were pregnant, lactating, or carrying an infant. 3) Does daily nutrient intake differ with age, sex and social status? I predicted that juveniles and high ranking monkeys would have greater protein intake per kg of metabolic body mass than adults and low ranking monkeys, respectively. For the same reasons described in question 2, no differences were expected in the nutrient intake of adult females and the adult male.

4.3 Materials and Methods

4.3.1 Animals and Study Site

The spider monkeys included in this study are part of the troop on display at the Auckland Zoo (New Zealand). At the time of the study, the troop consisted of 16 individuals. There were two geriatric females, one in her 40's (exact age is unknown due to lack of records) and one approaching 40. Other adult females in the troop ranged from around 5 to 22 years old. There were 2 adult males: the 12 year old alpha male and a 6 years old de-sexed male. The troop had two 2-year old juveniles, one male (de-sexed) and one female. Of the 16 troop members, nine individuals were focal animals in this study. The focal animals include individuals varying in sex, age, and social status. Information of the social status of individuals was provided by caretakers and was based upon observations on the monkeys' behaviour and

social interactions. None of the females in the study were lactating or pregnant and both juveniles had high ranking mothers. The identity and attributes of the focal animals are listed in table 4.1.

Table 4.1 The sex, age, and social status of the focal individuals.

Name	Sex	Age Class	Social Status
Basco	Male	Adult	High
Bunny	Female	Geriatric	High
Helga	Female	Geriatric	High
Bella	Female	Adult	High
Kelly	Female	Adult	High
Helen	Female	Adult	Low
Buenos	Female	Adult	Low
Kortez	Male	Juvenile	N/A
Julietta	Female	Juvenile	N/A

The troop has an off-view den that consists of four connected rooms, two rooms are outside and partially covered and the other two rooms are inside the building. The inside and outside rooms are connected with slide doors that can be used to grant or cut off access to respective parts of the den. The den is connected to their island, which is the public viewing area, by a raceway. Access to the raceway, and hence the ability to move between the island

and den, varies depending on factors such as the weather and the cleaning and setting up of the island or denning area.

4.3.2 Feeding Routine

The monkeys were fed in various locations: on the island, in the raceway, and in the dens. Feedings in the raceway typically occurred in ‘recalls’, during which the keeper would call them to the raceway and shut the slide door to the island once all 16 monkeys were in the raceway. Feeding in the den typically occurred at the end of the day or during inclement weather. On most days, all foods offered to the monkeys were consumed during the observation period except that of the final feed of the day when the facility was closed before the food was completely consumed. The monkeys were fed 5 times a day on average and feeding times were variable. Food delivery to the troop was also variable with the day’s worth of any particular food item sometimes being given all at once during one feed and sometimes being split between multiple feeds.

The monkeys were fed a range of fruits, vegetables, boiled chicken eggs and dog biscuits (Hill’s Science Diet – Adult Light). The daily diet changed each day during the week but was repeated weekly except some food used for behavioural enrichment (BE), which changed daily and repeated every four weeks. Additionally, the monkeys were occasionally given treats or one-off food items to facilitate the administration of medications. Food items such as carrots and parsnips were typically boiled in the microwave to facilitate their

consumption by the two geriatric members of the troop. All food items (regular, BE, treats) and their nutritional content (% of dry matter) are listed in Appendix 1, table A1.4.

4.3.3 Data Collection

Data were collected from April through September 2013 and consisted of 34.09 hours of observations. The adult male was observed for five days while all other focal animals were observed for three days. Focal animal sampling was used in this study to determine the quantity of daily food and nutrient intake of the focal individuals. Observations began at the first feed around 09:00 and ended around 16:30. Although some food remained in the exhibit at the end of the day, at least 80% of their daily diet was offered before the day's final feed (as the daily diets were typically spread out over 5 feeds) and were thus included in observations. The focal animal was followed during each feeding bout and continuous feeding data were collected from the time food was given until the point when all food was taken and the individual switched to a different activity. When the monkeys fed on the island, there were three main viewing spots that were utilized (the front of the island, the north side, and the back viewing platform). During recalls, viewing of monkeys was not allowed until all monkeys were inside and the slide door was shut as the presence of any additional people in the area could disrupt the process. Once all animals were inside, observations of feeding were allowed in the raceway. Preliminary observations revealed that feeding outside of the feeding bouts, such as on scraps, invertebrates, plants, etc. was minimal; such feeding was not included in data collection and analysis.

Food items were cut up into pieces before being distributed to the animals. The average weight of a 'piece' of each food item was determined by weighing 10 randomly selected. The average weight and the number of pieces of the food item consumed by each focal individual were used to estimate the weight consumed of each food item.

The time each focal animal devoted to feeding (searching, handling, and masticating food) was recorded to the nearest second and summed each day. Different components of food items were recorded separately (e.g. leafy parts vs. stalky parts of vegetables). When visibility was poor, the minimum amount of food that could be confidently assumed to be eaten was recorded (e.g. when offered a scatter of seeds, it was not always possible to see the number of seeds entering the mouth each time the hand was brought to the mouth. One seed was thus recorded). These data thus reflect the minimum amount of food consumed. If the focal animal went out of view during a feeding bout, the duration was recorded to calculate the proportion of the feeding time for which data were obtained. The average amount of time that each focal animal was in view during daily feeding events ranged from 86% to 98% (average: 91% +/- 1%). When the focal individual was seen carrying one particular food item to an area that was out of the view, I assumed the whole item was consumed and an estimated amount of food consumed was calculated using the feeding rate recorded for the particular food item from the individual during another feed session.

4.3.4 Nutritional Analysis

The following nutrients were included in the dietary analysis of the focal animals: protein, lipids, water soluble carbohydrates (WSC), starch, acid detergent fibre (ADF), and ash. Other components such as neutral detergent fibre and plant secondary metabolites were not included due to data not being available for all foods and due to financial constraints limiting the number of assays that could be completed in our lab. Data on the crude protein (CP), lipid, water soluble carbohydrates (WSC), starch, acid detergent fibre (ADF), and ash content of foods consumed by the focal animals were collected from the following sources: Zootrition (Wildlife Conservation Society, 1999), published data (Al-Sayed & Ahmed 2013; Belitz et al. 2009; Fuller 2004; Ghaly & Alkoaik 2009; Schmidt et al. 2005; van Huis et al. 2013), product suppliers, product nutrient labels, and from the national nutrient databases of the following: USA (<http://ndb.nal.usda.gov>), Canada (<http://www.hc-sc.gc.ca/fn-an/nutrition/fiche-nutri-data/index-eng.php>), Australia and New Zealand (<http://www.foodcomposition.co.nz/nip-database>), (<http://www.foodstandards.govt.nz/science/monitoringnutrients/nutrientables/pages/default.aspx>), and the UK (<http://www.food.gov.uk/science/dietarysurveys/dietsurveys>).

Additionally, nutrient analyses were carried out in the nutritional ecology lab at Massey University (Albany, New Zealand) for the components that were not available from other sources. All samples were placed in an oven at 60°C until dry and were then ground using a Wiley Mill. Samples for the starch assay were ground through a 0.5 mm screen while samples

for all other assays were passed through a 1 mm screen. Ground samples were stored at -20°C in individual sealable bags.

Dry matter was determined by drying ~500 mg of ground, semi-dry sample at 105 °C for 16 hours (Rothman et al. 2012). The Kjeldahl method (AOAC 2005) was used to determine the total nitrogen content of the food items which was then multiplied by 6.25 to yield the crude protein portion of the food items (AOAC 2005). Water soluble carbohydrates (WSC) content was determined using the Anthrone method as described in Total Carbohydrates Protocol (<http://web.itu.edu.tr/~dulekgurgen/Carbs.pdf>) and the Megazyme Total Starch Assay Kit was used to determine starch content using Megazyme Total Starch Assay Procedure (Megazyme, Bray, Ireland). The Mojonnier method (AOAC 954.02) was used to determine lipid content and ash content was determined using a dry ashing procedure (AOAC 920.153). ADF content was determined using the guidelines of ANKOM Technology (ADF Method 5). To determine the amount of available protein in their food items, the amount of protein bound to the ADF portion of each food item was determined using the Kjeldahl method (Rothman et al. 2008a). The amount of ADF-bound protein was then subtracted from the amount of crude protein in the food items to give the amount of available protein (hereinafter referred to as 'protein'). For statistical analyses, starch and WSC values were combined and are collectively referred to as non-structural carbohydrates. All analyses were based on the percentage of nutrients per dry matter.

4.3.5 Data Analysis

The non-protein energy (NPE) (non-structural carbohydrates plus lipids) to available protein energy (APE) ratio was calculated for the foods that made up 85% of the focal animals' diet (by weight). The NPE to APE ratio was also calculated for their daily macronutrient ratio intake. The NPE:APE ratio of their main foods was compared with that of their average daily intake to determine whether their foods all had a similar NPE:APE ratio and hence defined their macronutrient intake. The following factors were multiplied by the weight in grams consumed of the respective macronutrient to determine the energetic contribution of protein, lipids, and non-structural carbohydrates to their foods and daily intake: protein: 16.7 kJ, lipids: 37.7 kJ, and non-structural carbohydrates: 16.7kJ (National Research Council 1989).

The average weight of food consumed per day was determined for each individual. This is referred to as their food consumption unit (FCU) and was calculated using the following equation:

$$FCU = \frac{\sum_{i=d1}^n gFi}{n}$$

Where gF = grams of food consumed on day *i* and n = the number of days of observations.

The weight of protein, lipids, non-structural carbohydrates, ADF, and ash consumed each day by each focal animal were also calculated. Data on the available protein content of 4 food items (peanut butter, strawberry and apricot preserves, and watermelon rind), which collectively made up 1.02% of the focal animals' diet by weight, were unavailable so crude protein content was used.

Daily food and nutrient intake was compared between subsets of this troop based on age class (juvenile, adult, geriatric), sex (female, male), and social status (high, low). As food and nutrient intake are greatly determined by an animal's size (Nagy 2005), all food and nutrient measurements were divided by each individual's metabolic body mass ($M^{.762}$) (Rothman et al. 2008b). The body weight of all focal animals was estimated with the assistance of their keepers using weights on file at the Auckland Zoo. The two juveniles were not included in rank or sex analyses.

A linear regression was performed to determine the strength of the relationship between the focal animals' daily non-protein energy and protein energy intake (IBM SPSS 21). Permanova (Permanova+; Primer6) was used to test for differences in FCUs while both PERMANOVA and General Linear Model (GLM) (IBM SPSS 22) were used to investigate the daily nutrient intake between subsets based on age, sex, and rank. For all analyses conducted using Permanova, the Euclidean distance was used in production of the resemblance matrix and all data were square root transformed prior to production of the resemblance matrix.

4.4 Results

4.4.1 Macronutrient Composition of Food Items and Macronutrient Intake of the Focal Group

The NPE to APE ratio of the foods that made up 85% of our focal animals' diet ranged from 0.3 to 85.1, indicating a wide nutrient space is provided (Figure 4.1a). The average NPE to APE ratio consumed by the focal animals on a daily basis was 3.70 (Figure 1a). The daily

macronutrient intake of focal animals was maintained at a fairly consistent NPE (kJ) to APE (kJ) ratio ($R^2=0.661$) (Figure 4.1b). There is no evidence that a specific nutrient was prioritised.

4.4.2 Grams of Food Consumed Per Day

No difference was detected in the FCU between adult monkeys and geriatric monkeys (pseudo-f=0.9, $P=0.369$) (figure 4.2a). However, the juveniles had a significantly greater FCU than both adults (pseudo-f=21.4, $P=0.001$) and geriatric individuals (pseudo-f=5.1, $P=0.043$) (figure 4.2b). No differences were detected in the daily FCU between the adult females and adult male (pseudo-f= 4.6×10^{-2} , $P=0.821$) or between high ranking and low ranking individuals (pseudo-f=2.3, $P=0.131$) (figure 4.2c).

4.4.3 Daily Nutrient Intake Based on Age, Sex, and Social Status

Juveniles consumed significantly more of each tested nutrient per kg of metabolic body mass per day than adults (PERMANOVA: AP: pseudo-f=27.1, df=22, $P=0.001$; lipids: pseudo-f=6.5, df=22, $P=0.024$; non-structural carbohydrates: pseudo-f=10.1, df=22, $P=0.01$; ADF: pseudo-f=12.0, df=22, $P=0.003$; ash: pseudo-f=15.0, df=22, $P=0.004$) (GLM: AP: $F=27.471$, df=22, $P=0.000$; Lipids: $F=6.883$, df=22, $P=0.016$; NSC: $F=10.977$, df=22, $P=0.003$; ADF: $F=11.407$, df=22, $P=0.003$; Ash: $F=13.936$, df=22, $P=0.001$). Juveniles also consumed more protein, lipids, ADF, and ash than geriatrics (PERMANOVA: AP: pseudo-f=17.1, df=22, $P=0.003$; lipids: pseudo-f=7.7, df=22, $P=0.037$; ADF: pseudo-f=7.0, df=22, $P=0.019$; ash: pseudo-f=8.49, df=22, $P=0.017$) (GLM: AP: $F=14.525$, df=22, $P=0.003$; Lipids: $F=7.321$, df=22, $P=0.022$; ADF: $F=6.002$, df=22, $P=0.034$; Ash: $F=7.953$, df=22, $P=0.018$) (Table 4.2).

No difference was detected in the daily intake of non-structural carbohydrates between juveniles and geriatrics, however (PERMANOVA: pseudo-f=2.3, df=22, P=0.134; GLM: F=2.125, df=22, P=0.176). Daily nutrient intake did not differ between adults and geriatrics (PERMANOVA: AP: pseudo-f=0.37, P=0.575; lipids: pseudo-f=1.6, P=0.209; non-structural carbohydrates: pseudo-f=0.4, P=0.526; ADF: pseudo-f=0.4, P=0.541; ash: pseudo-f=0.3, P=0.573) (GLM: AP: F=0.282, df=22, P=0.601; Lipids: F=1.367, df=22, P=0.255; NSC: F=0.593, df=22, P=0.450; ADF: F=0.157, df=22, P=0.696; Ash: F=0.224, df=22, P=0.641) (Table 4.2). The amount of nutrients consumed each day in absolute terms by each subset is in

Table 4.3

No statistical differences in the daily intake of nutrients were detected between males and females (PERMANOVA: AP: pseudo-f=0.6, P=0.431; lipids: pseudo-f= 7.1×10^{-2} , P=0.41; non-structural carbohydrates: pseudo-f=0.7 P=0.41; ADF: pseudo-f=2.8, P=0.101; ash: pseudo-f=0.7, P=0.416) (GLM: AP: F=0.612, df=22, P=0.443; Lipids: F=0.120, df=22, P=0.733; NSC: F=0.369, df=22, P=0.550; ADF: F=2.525, df=22, P=0.127; Ash: F=0.758, df=22, P=0.394) (Table 4.2). The amount of nutrients consumed each day in absolute terms by each subset is in Table 4.3

No significant differences in daily nutrient intake were detected between high and low-ranking monkeys (PERMANOVA: AP: pseudo-f=0.4, P=0.524; lipids: pseudo-f=0.3, P=0.609; non-structural carbohydrates: pseudo-f=2.0, P=0.155; ADF: pseudo-f=0.1, P=0.732; ash:

pseudo-f=0.4, P=0.537) (GLM: AP: F=0.536, df=22, P=0.472; Lipids: F=0.120, df=22, P=0.733; NSC: F=1.890, df=22, P=0.184; ADF: F=0.209, df=22, P=0.652; Ash: F=0.469, df=22, P=0.501) (Table 4.2). The amount of nutrients consumed each day in absolute terms by each subset is in Table 4.3

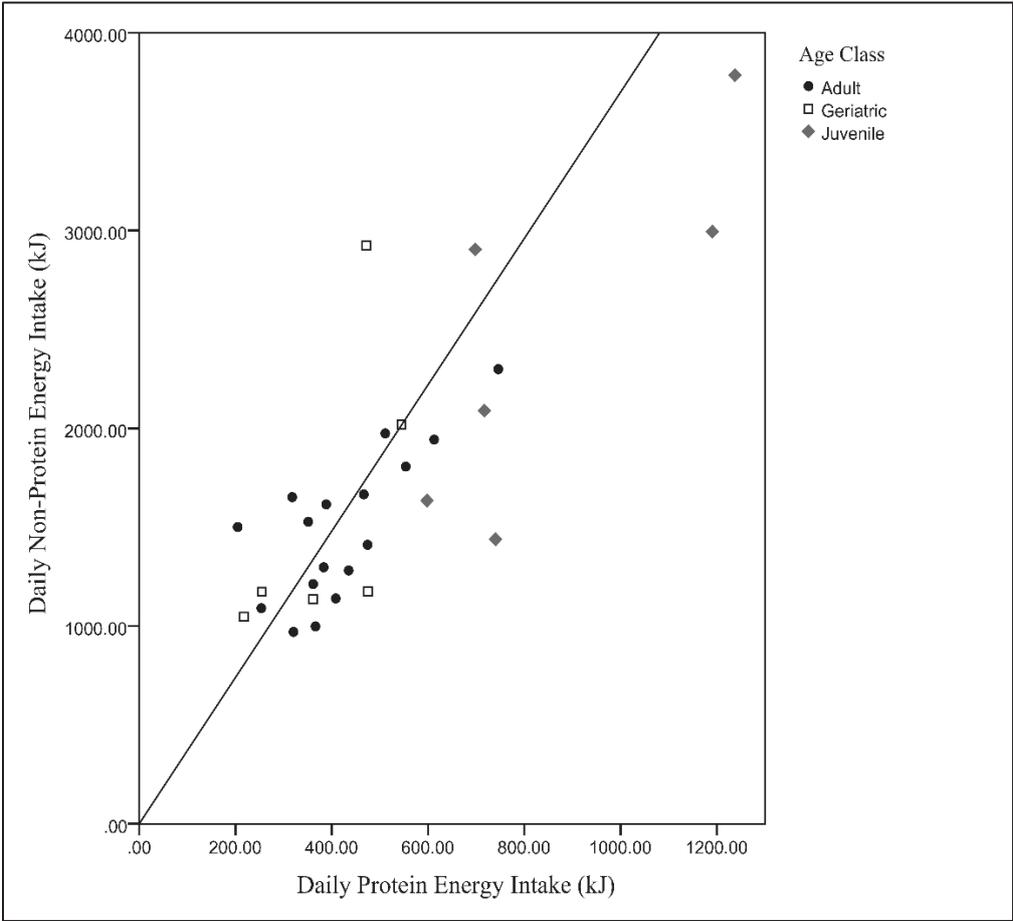
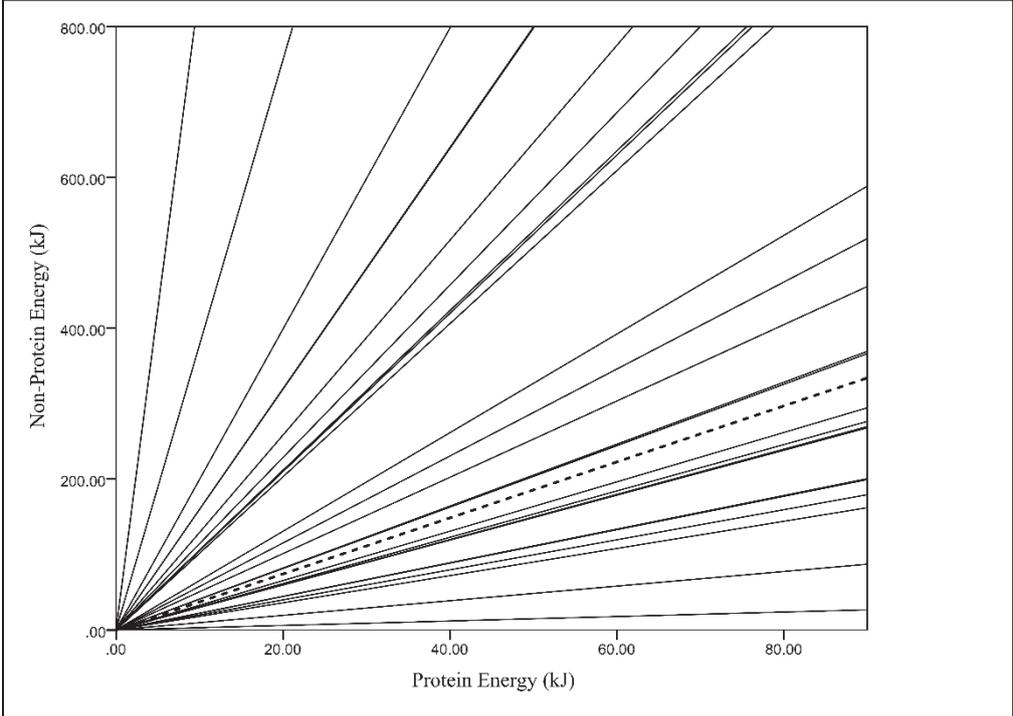


Figure 4.1 (Top) The NPE to APE ratio of each food item consumed by the focal individuals. Each solid line shows the NPE to APE ratio of one food item. Only foods that made up 85% of their diet are shown. The dotted line represents the average daily non-protein energy to protein energy ratio consumed by the focal animals. The ratio of their foods ranged from 0.3 to 85.1 while the focal animals consumed an average ratio of 3.70 NPE: 1 APE. (Bottom) The daily intake of non-protein energy (kJ) vs. available protein energy (kJ) for all focal animals (per kg of metabolic body mass). The straight line represents the average non-protein energy to available protein energy ratio intake of the focal animals.

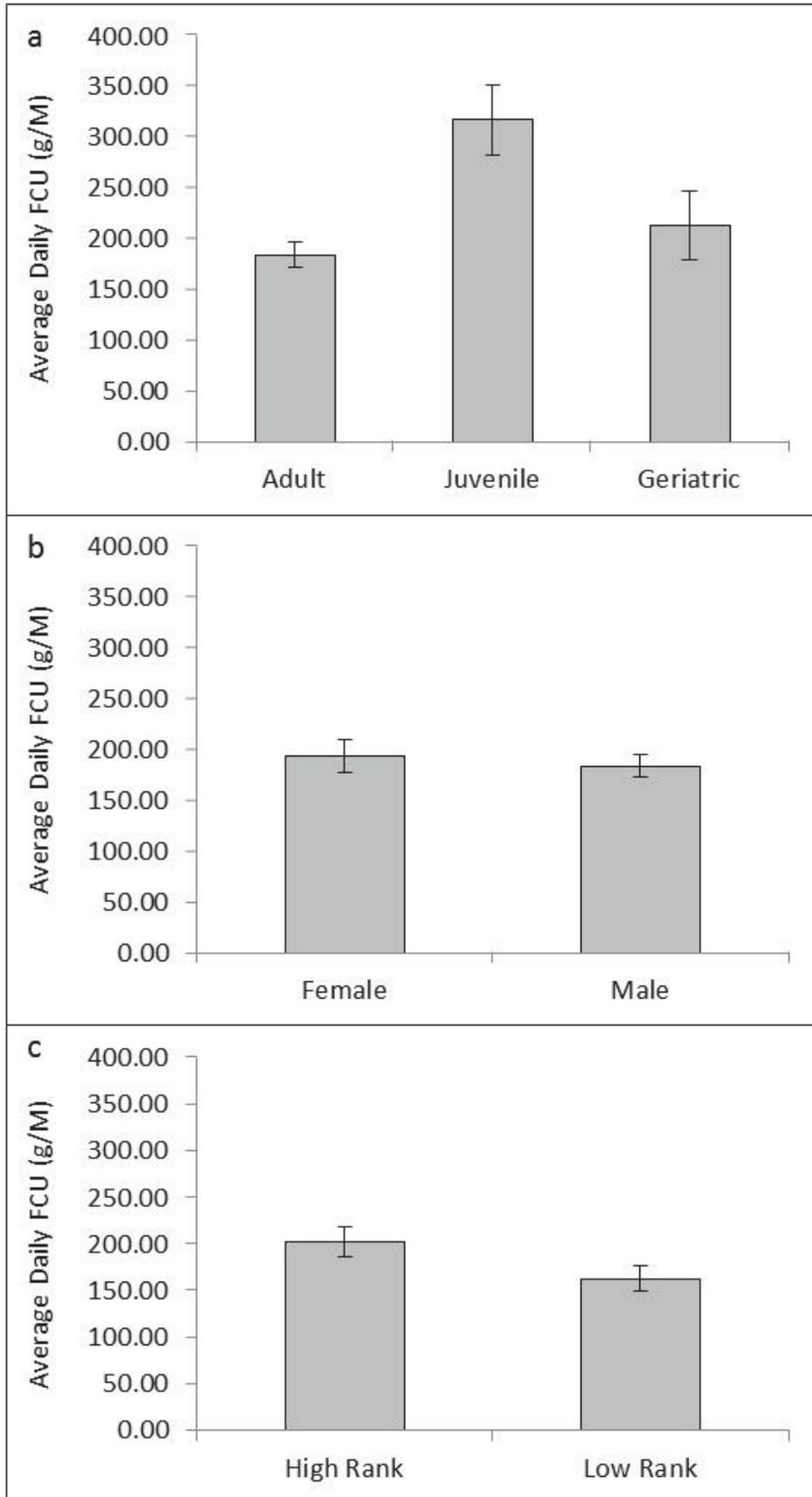


Figure 4.2 The average daily food consumption unit (FCU) (g of food consumed per kg of metabolic body mass) of the focal animals based on (a) age, (b) gender, and (c) social rank. The only significant differences are between juveniles and adults (pseudo-f=21.4, P=0.001) and between juveniles and geriatrics (pseudo-f=5.1, P=0.043). No differences were found between adults and geriatrics: (pseudo-f=0.9, P=0.369), females (adult and geriatric) and the adult male (pseudo-f=4.6x10⁻², P=0.821), or between high ranking and low ranking individuals (pseudo-f=2.3, P=0.131).

4.5 Discussion

This study was a novel investigation into the nutritional ecology of a fully captive spider monkey troop. Understanding captive animal food and nutrient intake and whether it is possible to offer diets that are not nutritionally constraining is critical for captive animal husbandry. This is particularly the case with animals, such as spider monkeys, that are ubiquitous in zoological institutions. The spider monkeys at the Auckland Zoo were provided with a diet that ranged widely in macronutrient ratio and they consumed a relatively stable macronutrient ratio each day (3.70). The lack of nutrient prioritization in their daily macronutrient intake indicates provided foods do not impose constraints. This is likely due to the nutritionally diverse diet that they are offered. Although such a regular nutrient intake pattern may suggest that the animals were restricted by the offered diet and hence had an intake that merely reflected the nutrient ratio that was made available to them, a crude estimate of nutrient availability based

Table 4.2 The average amount (grams) of each nutrient consumed per day per kg of metabolic body mass, \pm standard error, by each subset of the troop. The number in parentheses is the number of focal animals in each group. * = significant difference between juveniles and adults ($P < 0.005$); + = significant difference between juveniles and geriatrics ($P < 0.005$).

	AP*+	Lipids*+	NSC*	ADF*+	ASH*+
Juveniles (2)	51.71 \pm 6.75	15.28 \pm 2.15	113.69 \pm 19.62	37.47 \pm 6.23	20.32 \pm 2.32
Adults (5)	25.20 \pm 1.93	10.12 \pm 0.90	66.56 \pm 5.18	19.73 \pm 2.27	11.28 \pm 1.19
Geriatrics (2)	23.20 \pm 3.22	8.03 \pm 1.59	76.44 \pm 16.37	21.34 \pm 2.13	12.34 \pm 1.62
Adult Females (6)	23.35 \pm 1.90	9.72 \pm 0.94	67.33 \pm 7.02	21.57 \pm 2.10	12.00 \pm 1.19
Adult Male (1)	22.24 \pm 3.13	9.04 \pm 1.46	75.67 \pm 4.42	15.04 \pm 1.32	9.96 \pm 0.85
High Ranking (5)	25.39 \pm 2.05	9.41 \pm 1.02	73.61 \pm 7.00	20.64 \pm 2.26	11.95 \pm 1.23
Low Ranking (2)	22.64 \pm 2.38	10.04 \pm 1.00	56.48 \pm 6.15	18.78 \pm 2.25	10.44 \pm 1.23

Table 4.3 The average amount (grams) consumed per day, \pm the standard error, by each subset of the troop. The number in parentheses is the number of focal animals in each group.

	AP	Lipids	NSC	ADF	ASH
Juveniles (2)	143.01 \pm 18.67	42.25 \pm 5.95	314.42 \pm 54.26	103.64 \pm 17.23	56.19 \pm 6.43
Adults (5)	119.40 \pm 7.86	46.86 \pm 4.13	337.00 \pm 28.51	95.90 \pm 7.37	55.42 \pm 4.22
Geriatrics (2)	105.81 \pm 17.33	36.87 \pm 8.17	348.38 \pm 82.85	96.27 \pm 11.58	55.77 \pm 8.29
Adult Females (6)	116.86 \pm 8.89	45.37 \pm 4.49	309.10 \pm 33.03	98.38 \pm 9.19	54.82 \pm 5.27
Adult Male (1)	128.54 \pm 18.09	52.26 \pm 8.47	437.42 \pm 25.56	86.97 \pm 7.64	57.57 \pm 4.89
High Ranking (5)	124.44 \pm 9.76	46.95 \pm 5.43	363.39 \pm 35.43	98.98 \pm 9.32	57.88 \pm 5.30
Low Ranking (2)	105.14 \pm 11.07	46.64 \pm 4.63	262.22 \pm 28.54	87.18 \pm 10.47	48.45 \pm 5.71

on average weights of foods items suggests otherwise. The NPE to APE ratio of the foods that made up at least 50% of their daily diet (by weight) are spread out (ranging from 0.81 to 37.78) and not focused near the average intake ratio of the focal animals. These data suggest that the macronutrient intake of our focal animals was not restricted by the offered diet. The extent to which their intake patterns reflect their physiological requirements remains to be determined, however. Experimental studies testing their food choice under different nutritional constraints (e.g. Hewson-Hughes et al. 2013; Hewson-Hughes et al. 2011), and relating such nutrient intake patterns to health and other components of fitness (e.g. Lee et al. 2008; Raubenheimer & Jones 2006), are required to address this.

The range of macronutrient composition in available foods as well as the macronutrient balance sought by the captive monkeys differs from that of wild Peruvian spider monkeys. The NPE to APE ratio in the common foods of the wild troop ranged from 1.18 to 33.33 and they sought a balance of 8:1 in their macronutrient intake (Felton et al. 2009b; Felton et al. 2009c) while captive foods' NPE to APE ratio ranged from 0.29 to 85.1 and the captive monkeys maintained a NPE to APE intake ratio of 2.28:1. It is unlikely that this difference is due to a biased nutrient composition of provided foods in captivity as captive foods were highly variable in macronutrient composition. The captive monkeys were hence not restricted to the daily macronutrient ratio which they were observed to consume. Although further research on this is required, it is possible that such a difference between the two species reflects variation in

nutritional goals between species, despite a close phylogenetic relationship. Such a difference in macronutrient ratio intake may also be due to different activity levels between captive and wild monkeys. Wild spider monkeys (multiple species) travel an average of 2 km a day (see Suarez 2006). Captive animals clearly do not travel as much and thus may have different energetic requirements which could affect their nutrient intake. Although few studies can be found that directly compare the nutrient intake of wild and captive conspecifics, a short-term study on human males during active and sedentary periods show that a decrease in energy expenditure did not result in a decrease in energy intake or appetite (Stubbs et al. 2004), suggesting there may not be a difference. However, the long term effects of a more sedentary lifestyle or effects of being born into a more sedentary lifestyle on nutrient and energy intake remain to be determined.

Juveniles consumed more food (and hence more nutrients) per kg of metabolic body mass than adult and geriatric monkeys. This is in alignment with other studies and theories on the nutritional requirements of juveniles. Juvenile mountain gorillas, while consuming the same macronutrient balance as adults (Rothman et al. 2011b), consumed more protein and more food than adult males per kg metabolic body mass (Rothman et al. 2008b). Juvenile black howler monkeys (*Alouatta pigra*) also consume more protein than adult males (Amato et al. 2014). Sufficient protein is important for growing juveniles and protein deficiency has been shown to cause weight loss, hair loss, muscular wasting, and pancreatic damage in juvenile

monkeys in laboratory conditions (Chopra et al. 1987; Racela Jr et al. 1966). This has implications for captive environments as efforts should be made to ensure that juveniles have access to enough quality food items. Ensuring that provided foods are small, and hence cannot be easily usurped, and are spread out enough to prevent monopolization (Chancellor & Isbell 2008; Mathy & Isbell 2001) are effective ways to ensure juveniles, and others, have equitable access to foods during social feeding.

No differences were detected between the food and nutrient intake of male and female monkeys. This may be because none of the adult females in the focal group were pregnant or lactating at the time of the data collection. Pregnancy, lactation, and the carrying of young are the reasons why females are expected to have greater nutrient requirements than males (Clutton-Brock et al. 1989; National Research Council 2003; Picciano 2003; Strier 2000; Tobey et al. 2006). Although one of the high ranking adult females in our study had a juvenile who she frequently held, she did not carry him over notable distances, also removing the effect of child carrying. Interestingly, no detectable differences were found between females, who were either pregnant or lactating, and males in the wild Peruvian spider monkey troop (Felton et al. 2009b). As investigating the effects of lactation and pregnancy on food and nutrient intake was not possible in this study due to the lack of females in varying reproductive states, future studies including pregnant, lactating, and cycling females would be beneficial towards understanding how these factors affect nutrient intake in females as compared with males.

Similarly, no differences in daily nutrient intake were detected between high and low ranking monkeys. Although studies on wild spider monkeys revealed that most aggression during feeding times flows from males to females and from females to recently immigrated females (Asensio et al. 2008; Fedigan & Baxter 1984; Slater et al. 2009), studies directly relating such aggression during feeding to social rank are lacking. It is thus not possible to know whether this trend in daily nutrient intake is representative of other spider monkey troops, captive or wild. While some aggressive interactions were observed in the zoo troop, such encounters did not lead to differences in food or nutrient intake between high and low ranking monkeys or between the adult male and the females. As discussed with regard to juveniles, offering small pieces of food and distributing items widely, as occurs at Auckland Zoo, is likely to help ensure that food acquisition is equitable in this troop.

There are some limitations which need to be considered when interpreting the results of this study. First, the use of published data for the nutrient concentrations of some of the monkeys' foods may have introduced error. Nutritional concentrations can vary between foods grown under different conditions, in different places, and in different times (Chapman et al. 2003). This particularly needs to be considered with respect to the comparison of the captive troop's daily NPE:APE ratio intake with that of the wild spider monkeys. Intragroup comparisons should not be affected by this limitation, however, as relative differences between individuals would be the same as the same data set was used for all focal animals. Another

limitation is the lack of multiple adult males in the troop and the lack of pregnant and lactating females. It is imperative that more males and pregnant and lactating females are included in future studies on this species. This will allow for a greater sample size of adult males and will allow for the comparison of food and nutrient intake between females differing in reproductive status. Additionally, although I was able to investigate whether their diet was nutritionally constrained through analysis of their daily macronutrient intake pattern, experimentally testing whether the ratio maintained in this study accurately represents the troop's nutritional goal was not possible as I was not allowed to interfere with the troop's husbandry. I highly suggest that such testing be included in future research if possible. Experimental determination and confirmation of their nutritional goals will further our understanding of this species' nutritional ecology in captivity and will enhance our general understanding of if and how nutritional goals vary under different circumstances.

Chapter 5: General Discussion and Conclusion

The overall aim of this study was to investigate food and nutrient intake in primates under three different levels of human dietary interference. This was of interest due to the conservation problems that primates face (e.g. habitat loss, hunting, trade (Estrada et al. 2017)) as well as the fact that many primates are at least partially dependent upon humans for food as a result of the use of provisioning and captivity in wildlife tourism. Knowledge on primate food and nutrient intake is essential if we are to protect and rebuild their habitats and if we are to continue to feed them for tourism purposes. With such knowledge, essential resources can be protected in the wild and nutritionally appropriate diets can be formulated in captive and semi-captive situations, all having implications for the conservation and welfare of these animals. Understanding food and nutrient intake within group is also important as differences may exist between conspecifics due to factors such as age (National Research Council 2003), sex (Altmann & Samuels 1992; Clutton-Brock et al. 1989; Picciano 2003), reproductive status (McCabe & Fedigan 2007), and social rank (Janson 1990; Robinson 1981). Intra-troop food and nutrient intake patterns were thus included in this study.

5.1 Wild Golden Snub-nosed Monkeys

The wild golden snub-nosed monkeys in this study consumed many different plant species and one fungal species during the observation period. Of all species consumed, a small number of species made a notable contribution to their diet. These species are *Morus alba*,

Cornus spp, *Pinus massoniana*, *Lindera obtusiloba*, *Grewia biloba*, *Quercus aliena*, *Litsea rubescens*, and *Padus asiatica*. The importance of these species to snub-nosed monkeys should be taken into account in habitat protection and restoration projects.

A positive correlation between food species availability and dietary contribution was not found, suggesting that these monkeys are selecting these plants for other reasons such as nutritional content. Analysis of the crude protein, non-protein (lipids and non-structural carbohydrates), and neutral detergent fibre ratio of their main dietary items compared with other foods does not suggest that they are focusing on foods that are necessarily high or low in any of these components or at a specific balance, however. Instead, most of their main foods are found on the perimeter of the nutrient space occupied by all foods. Further research into the nutritional composition of their foods in different areas and during other seasons are required to expand upon these results. Non-foods should be included in future studies as patterns may emerge upon comparison of such plants with those that are consumed. For example, foods of a golden snub-nosed monkey troop in Hubei Province were lower in fibre than non-foods yet protein content and the protein to fibre ratio did not differ between the foods and non-foods (Liu et al. 2013). The Hubei province troop also did not appear to be deterred by secondary plant metabolites (Liu et al. 2013), a pattern also found in another colobine monkey, the Tana River red colobus monkey (*Procolobus badius rufomitratu*s) (Mowry et al. 1996). Secondary plant metabolite intake differed slightly in another colobine species, the

silver leaf monkey (*Trachypithecus auratus sondaicus*) as consumed fruits had a greater secondary metabolite content than non-consumed fruits while the opposite was true for leaves (Kool 1992). Determining the differences between favoured foods, other foods, and non-foods will help us understand the nutritional basis of food selection in these animals.

Future studies should also consider researching their nutrient intake and their foods' nutrient composition on a more detailed time scale. A study on mangabeys (*Lophocebus albigena*) revealed the nutritional patterns behind their food choices through different developmental stages of a frequently consumed fruit, *Blighia unijugata* (Masette et al. 2015). Seeds, for example, were consumed during the stages in which tannin levels were relatively low but were then avoided once tannin levels increased (Masette et al. 2015). Determining not only what plants and parts are important to these monkeys, but also what developmental stages are consumed, is clearly necessary to broaden our understanding of this species' nutritional ecology.

Although their food choice did not reflect food availability, seasonal trends of nutrient consumption matched that of nutrient availability for crude protein, lipids, and non-structural carbohydrates, but not for neutral detergent fibre or lignin. Whether this was by choice or restriction remains to be determined. Future studies on this troop will help reveal whether this trend is consistent across years. Additionally, future studies on this species in general, which also analyse nutrient intake and availability, will broaden our understanding of how this species

interacts with its environment on a nutritional level and whether such patterns reflect choice, constraints, or both. Investigating micronutrient intake in this species would also be valuable as they are also crucial to animal health, as can be seen when they are over or under consumed in our own species (Black et al. 2008; DiPalma & Ritchie 1977).

No differences were detected in the consumption of species or plant parts between monkeys based on age, sex, or reproductive status. While this may indeed be the case, it is possible that such results are due to our small sample size and requires further investigation. On the nutritional level, results suggest age differences in proportional nutrient intake in golden snub-nosed monkeys with juveniles consuming more of all nutrients per metabolic body mass. These results are in alignment with the theory that juveniles, who are growing and developing, have greater nutrient requirements than adults (National Research Council 2003). Furthermore, adult females consumed more of all nutrients except lipids per metabolic body weight during summer than adult males. Such a higher nutrient intake may due to their greater energy expenditures for pregnancy, lactation, and infant carrying (e.g. Clutton-Brock et al. 1989; Picciano 2003; Strier 2000). The fact that a difference in lipid consumption was not detected between females and males during summer is interesting. One possibility is that females' lipid requirements surpass those of males when they are about to conceive, which occurs in autumn. This is also when temperatures drop in their seasonal environment and when food sources begin to decline in variety. Perhaps they increase their lipid consumption at this time to facilitate

pregnancy during such trying times. Although lactation is expected to be very energetically demanding, no differences in proportional nutrient intake were detected between lactating and non-lactating females. This, again, could be due to the small sample sizes.

These data on the nutrient intake trends of different subsets of a golden snub-nosed monkey population suggest differences in intake based on age and sex. The nutritional intake of these monkeys, their foraging habits, and the nutritional composition of their natural foods should collectively be taken into consideration when developing plans to preserve and restore their habitat. Furthermore, such data should be taken into consideration by people who manage members of this species in captivity or wildlife tourism parks in an effort to maximize the welfare of these monkeys.

5.2 Semi-wild and Provisioned Golden Snub-nosed Monkeys in a Wildlife Tourism Centre

I found significant differences in the nutrient composition of foods consumed by the two troops with the provisioned troop's foods being higher in non-structural carbohydrates and lipids and lower in neutral detergent fibre and lignin. Similarly, there were differences in the proportional nutrient intake between the provisioned group and the wild group. The provisioned monkeys' diet contained proportionally more non-structural carbohydrates and less crude protein, neutral detergent fibre, and lignin during both summer and autumn compared to that of the wild group. Proportional lipid intake was lower for the provisioned monkeys during summer and greater during autumn than that of the wild troop.

The first recommendation for this wildlife tourism site in terms of reducing the likelihood of this troop having a grossly imbalanced diet is to allow the monkeys to have greater access to natural foods. This can be accomplished through reducing the number of monkeys kept in the viewing area, thereby reducing the monkey density and hence reducing intraspecific competition and foraging pressure placed upon the plants. Furthermore, changing the location of the viewing area more frequently to prevent irreversible damage to the plants and allowing for regeneration, and ultimately re-use, is suggested. Even if such changes are made, it is likely that the monkeys will still require at least some provisioning. It is thus recommended that foods such as apples, bananas, and peaches, the most nutritionally imbalanced of their provisioned foods, be reduced in their diet. At the same time, providing foods that are not as vastly different from wild foods in macronutrient content is recommended. Such foods include beetroot, bok choy, cabbage, carrots, cucumber, and spinach. Whether providing such foods is feasible in terms of availability and finances needs to be considered, however.

These results show how animals fed an unnatural diet, a situation commonly found in wildlife tourism settings including captive environments such as zoos, has the potential to alter an animal's nutrient intake patterns. This is concerning as unbalanced diets can lead to a variety of health problems (e.g. Bremer et al. 2011; Cuzzo & Sauter 2006), affecting the animals' welfare. Further research is needed to determine if the health, fecundity, and longevity of these provisioned monkeys is impacted. It is important that operators of wildlife tourism businesses

recognize the potential impacts that an unnatural diet may have on animals and that they are provided with knowledge and guidelines, that will help them minimize this risk.

5.3 Captive and Fully Provisioned Black-handed Spider Monkeys in a Zoo

The results of our study suggest that the spider monkey troop at the Auckland Zoo is offered a diet that ranges widely in macronutrient composition and that the troop is not facing nutritional constraints. Had the troop been constrained, nutrient prioritization would have been detected in the daily macronutrient intake of the focal animals. These results suggest it is possible to formulate balanced diets, at least in terms of macronutrients, that are based on food items conventionally used in the zoos that would not make up this species' natural diet. Future studies on captive spider monkey nutrition should investigate their micronutrient intake as well. Studies on captive members of other species found some micronutrient deficiencies which could impact their health. Captive woolly monkeys (*Lagothrix lagotricha*), for example, were suspected to have insufficient vitamin and mineral intake which could lead to various complications such as heart disease and diabetes (Ange-van Heugten et al. 2007). Similarly, a study on captive marine mammals noted vitamin E deficiencies and the over consumption of thiamin and vitamins A and D (Bernard & Ullrey 1989). Incorporating all factors into nutritional studies should thus be an endeavor in our efforts to understand animal nutrition. This will greatly broaden our knowledge in the area and improve our ability to care for provisioned animals in ways that are optimal for their welfare.

This study's findings also suggest that there are differences in nutritional intake patterns between juveniles and older monkeys (adults and geriatrics). Juveniles consumed more food and nutrients per metabolic body mass than adult and geriatric monkeys (asides from non-structural carbohydrate intake which did not differ between juveniles and geriatrics – see below). These results support the theory that juveniles have greater nutrient requirements due to the energetic expenses of growth and development (National Research Council 2003).

No differences were detected in the food or nutrient intake between the one adult male of the group and the adult/geriatric females. Results from studies on gender specific nutrient intake have not been consistent. Differences were found between the nutrient intake of male and female mountain gorillas (Rothman et al. 2008b) and golden snub-nosed monkeys (see chapter 2), for example, but not between male and female Peruvian spider monkeys (Felton et al. 2009b). It is possible that there are differences between male and female Peruvian spider monkeys but that such differences could not be detected under the constraints of field work. Males and females are expected to differ in their nutrient intake due to energetic costs that females have during pregnancy, lactation, and infant carrying (Clutton-Brock et al. 1989; National Research Council 2003; Picciano 2003; Strier 2000). It is possible that no differences were detected between the sexes in our study as none of the females were pregnant or lactating. And although one of the adult females was still carrying her son, these events were rare as he was maturing and carrying distances were never great due to their confinement. Additional

studies on captive members of this species and on breeding troops are required to investigate this aspect of their nutritional ecology. In addition to our study being limited by the lack of pregnant or lactating females, it was also limited in that there was only one intact adult male in the troop. Studies on the nutrient intake of other males living in groups of a similar social structure would be beneficial.

Interestingly, no differences in food or nutrient intake were detected between individuals differing in social rank. Unfortunately, detailed studies concerning rank related feeding success are lacking in wild spider monkeys. At best, we know that adult females are aggressive towards younger females, especially if they are recent immigrants, and that males direct aggression towards females (Asensio et al. 2008; Fedigan & Baxter 1984; Slater et al. 2009). Most female-female aggression occurs during feeding suggesting food competition (Slater et al. 2009). But how tightly this competition and aggression are related to social rank remains to be determined. One possible explanation for the lack of difference in nutritional intake between the ranks in our troop is how the food is prepared and distributed. Foods that are large in size and/or clumped in distribution are easy to be stolen or protected by dominant animals. During most feedings at the Auckland Zoo, foods were cut into multiple smaller pieces and were spread around, preventing stealing and monopolization. This likely enabled all troop members to have fair access to foods.

Factors other than nutrient requirements can influence food and nutrient intake, however. This may explain the lack of a difference in non-structural carbohydrate intake between juveniles and geriatrics. Bunny, the eldest member of the troop, was missing many teeth. It is likely that Helga, who was a few years younger, was also missing teeth or at least having some oral health complications. This limited the range of foods that were edible despite being 'available'. On one occasion, Bunny tried multiple times to crack open a peanut shell but could not and eventually gave up. Perhaps foods that were easier for these two geriatric monkeys to consume, i.e. foods that are softer such as soft fruits, tended to be higher in non-structural carbohydrates content. This could very well explain why their NSC intake did not differ from that of the juveniles. Such physical constraints which affect the actual availability of offered foods need to be considered. Keepers at Auckland Zoo made attempts to facilitate the two geriatric troop members by steaming root vegetables, making them easier to consume. Perhaps increasing the amount of steamed or otherwise softened vegetables offered would allow more choice for geriatric individuals and allow them to alter their nutrient intake. It is also important to consider whether there are health implications associated with elevated intake levels of non-structural carbohydrate. Qualitatively, these spider monkeys appear to be relatively healthy (e.g. physique, hair condition) and the two geriatric females exceeded the life expectancy of captive spider monkeys (Washburn 1981). They thus may not be over consuming

non-structural carbohydrates to the point of adverse health effects. Long term studies on more individuals are required to determine this, however.

In summary, this study has documented important foods in the habitat of a wild golden snub-nosed monkey troop and has shown that the focal troop's food choice is not correlated with food availability. While there is some overlap in plant usage with other studied troops of this species, there are also differences. Future studies on this species in the wild across different seasons and years, when combined with previous studies such as this study, will provide a bigger picture of how these monkeys interact with their habitat on a nutritional level across time and space. Food provisioning affected the proportional nutrient intake of this species due to the notable differences in nutritional composition between natural foods and provisioned foods. Captive black-handed spider monkeys, on the other hand, appear to be able to reach a balanced diet despite being fully provisioned as demonstrated by their daily nutrient intake patterns. With regards to intratrop nutrient intake patterns, results from both the golden snub-nosed monkeys and black-handed spider monkeys are in alignment with previous theories on the greater nutritional requirements of juveniles compares with adults. More rigorous research in nutritional intake based on sex are required for us to better understand the effect of sex on nutrient intake in animals. Differences were detected in the snub-nosed monkeys but not in the spider monkeys. Whether this is a result of methodologies used, species specific physiology, and/or environment remains to be determined. Similarly, further research is required to broaden

our understanding of the effect of female physiological status and social rank on nutritional intake. The results of this study have advanced our understanding of primate nutritional intake under differing levels of human interference and will contribute to our ongoing endeavor to understand the effect of various biological factors on animal nutrient intake.

Chapter 6: References

- Agricultural and Food Research Council. 1992. Nutritive requirements of ruminant animals: protein. *Nutrition Abstracts and Reviews Series B, Livestock Feeds and Feeding*:787-835.
- Al-Sayed, H. M., and A. R. Ahmed. 2013. Utilization of watermelon rinds and sharlyn melon peels as a natural source of dietary fiber and antioxidants in cake. *Annals of Agricultural Sciences* **58**:83-95.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* **49**:227-266.
- Altmann, J., and A. Samuels. 1992. Costs of maternal care: infant-carrying in baboons. *Behavioral Ecology and Sociobiology* **29**:391-398.
- Amato, K. R., S. R. Leigh, A. Kent, R. I. Mackie, C. J. Yeoman, R. M. Stumpf, B. A. Wilson, K. E. Nelson, B. A. White, and P. A. Garber. 2014. The role of gut microbes in satisfying the nutritional demands of adult and juvenile wild, black howler monkeys (*Alouatta pigra*). *American Journal of Physical Anthropology* **155**:652-664.
- Anderson, M. J. 2001. A new method for non - parametric multivariate analysis of variance. *Austral ecology* **26**:32-46.
- Ange-van Heugten, K., R. Burns, M. Verstegen, W. Jansen, P. Ferket, and E. Van Heugten. 2007. Evaluation of diabetes determinants in woolly monkeys (*Lagothrix lagotricha*). *Journal of Animal Physiology and Animal Nutrition* **91**:481-491.
- AOAC 2005. Official methods of analysis of AOAC International. AOAC International, Arlington.
- Asensio, N., A. H. Korstjens, C. M. Schaffner, and F. Aureli. 2008. Intragroup aggression, fission–fusion dynamics and feeding competition in spider monkeys. *Behaviour* **145**:983-1001.
- Basey, J. M., and S. H. Jenkins. 1995. Influences off predation risk and energy maximization on food selection by beavers (*Castor canadensis*). *Canadian Journal of Zoology* **73**:2197-2208.
- Bauchop, T., and R. Martucci. 1968. Ruminant-like digestion of the langur monkey. *Science* **161**:698-700.
- Behie, A. M., and M. S. Pavelka. 2012. Food selection in the black howler monkey following habitat disturbance: implications for the importance of mature leaves. *Journal of Tropical Ecology* **28**:153-160.
- Belitz, H.-D., W. Grosch, and P. Schieberle. 2009. Fruits and Fruit Products. Pages 807-861. *Food Chemistry*. Springer Berlin Heidelberg.
- Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology* **14**:105-134.

- Bergman, C. M., J. M. Fryxell, C. C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology* **70**:289-300.
- Berman, C. M., J. Li, H. Ogawa, C. Ionica, and H. Yin. 2007. Primate tourism, range restriction, and infant risk among *Macaca thibetana* at Mt. Huangshan, China. *International Journal of Primatology* **28**:1123-1141.
- Bermejo, M., J. D. Rodríguez-Teijeiro, G. Illera, A. Barroso, C. Vilà, and P. D. Walsh. 2006. Ebola outbreak killed 5000 gorillas. *Science* **314**:1564-1564.
- Bernard, J. B., and D. E. Ullrey. 1989. Evaluation of dietary husbandry of marine mammals at two major zoological parks. *Journal of Zoo and Wildlife Medicine*:45-52.
- Black, R. E., L. H. Allen, Z. A. Bhutta, L. E. Caulfield, M. De Onis, M. Ezzati, C. Mathers, J. Rivera, Maternal, and C. U. S. Group. 2008. Maternal and child undernutrition: global and regional exposures and health consequences. *The Lancet* **371**:243-260.
- Boubli, J.-P., Di Fiore, A., Stevenson, P., Link, A., Marsh, L. & Morales, A.L. 2008. *Ateles belzebuth*. The IUCN Red List of Threatened Species. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T2276A9384912.en>.
- Bremer, A. A., K. L. Stanhope, J. L. Graham, B. P. Cummings, W. Wang, B. R. Saville, and P. J. Havel. 2011. Fructose - fed rhesus monkeys: a nonhuman primate model of insulin resistance, metabolic syndrome, and type 2 diabetes. *Clinical and translational science* **4**:243-252.
- Browne, C. L., and S. J. Hecnar. 2007. Species loss and shifting population structure of freshwater turtles despite habitat protection. *Biological Conservation* **138**:421-429.
- Caan, B., D. M. Horgen, S. Margen, J. C. King, and N. P. Jewell. 1987. Benefits associated with WIC supplemental feeding during the interpregnancy interval. *The American Journal of Clinical Nutrition* **45**:29-41.
- Caliński, T., and J. Harabasz. 1974. A dendrite method for cluster analysis. *Communications in Statistics-theory and Methods* **3**:1-27.
- Cant, J. G. 1990. Feeding ecology of spider monkeys (*Ateles geoffroyi*) at Tikal, Guatemala. *Human Evolution* **5**:269-281.
- Carlson, B. A., J. M. Rothman, and J. C. Mitani. 2013. Diurnal variation in nutrients and chimpanzee foraging behavior. *American Journal of Primatology* **75**:342-349.
- Caton, J. M. 1998. The morphology of the gastrointestinal tract of *Pygathrix nemaeus* (Linnaeus, 1771). Pages 129-152 in Jablonski N. G., editor. *The Natural History of the Doucs and Snub-nosed Monkeys*. World Scientific Publishing, Singapore.
- Chancellor, R. L., and L. A. Isbell. 2008. Punishment and competition over food in captive rhesus macaques, *Macaca mulatta*. *Animal Behaviour* **75**:1939-1947.
- Chang, Z. F., M. F. Luo, Z. J. Liu, J. Y. Yang, Z. F. Xiang, M. Li, and L. Vigilant. 2012. Human influence on the population decline and loss of genetic diversity in a small and isolated

- population of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *Genetica* **140**:105-114.
- Chapman, C. A., L. J. Chapman, K. D. Rode, E. M. Hauck, and L. R. McDowell. 2003. Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology* **24**:317-333.
- Chapman, C. A., L. J. Chapman, R. Wingham, K. Hunt, D. Gebo, and L. Gardner. 1992. Estimators of fruit abundance of tropical trees. *Biotropica*:527-531.
- Chapman, C. A., L. J. Chapman, A. E. Zanne, J. R. Poulsen, and C. J. Clark. 2005. A 12-year phenological record of fruiting: implications for frugivore populations and indicators of climate change. Pages 75-92 in Dew J. L. and Boubli J. P. editors. *Tropical Fruits and Frugivores*. Springer, USA.
- Chapman, C. A., and J. F. Gogarten. 2012. Primate conservation: is the cup half empty or half full. *Nature Education Knowledge* **4**:7.
- Chaves, Ó. M., K. E. Stoner, V. Arroyo-Rodríguez, and A. Estrada. 2011. Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in southern Mexico. *International Journal of Primatology* **32**:177-192.
- Chaves, O. M., K. E. Stoner, and V. Arroyo - Rodríguez. 2012. Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico. *Biotropica* **44**:105-113.
- Chen, F. 1983. An observation on the behavior and some ecological habits of the Golden Monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains. *Acta Theriologica Sinica* **3**:141-146.
- Chivers, D. J., and C. M. Hladik. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *Journal of morphology* **166**:337-386.
- Chopra, J., J. Mehta, S. Rana, U. Dhand, and S. Mehtal. 1987. Muscle involvement during postnatal protein calorie malnutrition and recovery in rhesus monkeys. *Acta Neurologica Scandinavica* **75**:234-243.
- Clauss, M., and J.-M. Hatt. 2011. Greengrocery guide. *Zooquaria*:22-23.
- Clutton-Brock, T., S. Albon, and F. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature* **337**:260-262.
- Conklin-Brittain, N. L., Knott, C. D., and Wrangham, R. W. 2006. Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. Pages 445-471 in Hohmann G., Robbins, M. M., and Boesch C., editors. *Feeding Ecology in Apes and Other Primates. Ecological, Physical and Behavior Aspects*. Cambridge University press, Cambridge, U.K.

- Cork, S. J. 1996. Optimal digestive strategies for arboreal herbivorous mammals in contrasting forest types: why koalas and colobines are different. *Australian Journal of Ecology* **21**:10-20.
- Corlett, R. T., and P. Lucas. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia* **82**:166-171.
- Cuarón, A. D., A. Morales, A. Shedden, E. Rodríguez-Luna, P. C. de Grammont, and L. Cortés-Ortiz. 2008. *Ateles geoffroyi*. The IUCN Red List of Threatened Species. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T2279A9387270.en>.
- Cuarón, A. D., Shedden, A., Rodríguez-Luna, E., de Grammont, P.C. & Link, A. 2008. *Ateles fusciceps*. The IUCN Red List of Threatened Species 2008. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T135446A4129010.en>.
- Cuozzo, F. P., and M. L. Sauther. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *Journal of Human Evolution* **51**:490-505.
- Davies, A., E. L. Bennett, and P. G. Waterman. 1988. Food selection by two South - east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society* **34**:33-56.
- Dew, J. L. 2005. Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*. *International Journal of Primatology* **26**:1107-1135.
- Di Fiore, A., and C. J. Campbell. 2007. The atelines: variation in ecology, behavior, and social organization. Pages 155-185 in Campbell C.J., editor. *Primates in Perspective*. Oxford University Press, U.K.
- DiPalma, J. R., and D. M. Ritchie. 1977. Vitamin toxicity. *Annual Review of Pharmacology and Toxicology* **17**:133-148.
- Dobson, A. P., A. Bradshaw, and A. á. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* **277**:515-522.
- Dubois, S., and D. Fraser. 2013. A framework to evaluate wildlife feeding in research, wildlife management, tourism and recreation. *Animals* **3**:978-994.
- Dudley, N. 2008. Guidelines for applying protected area management categories. Gland, Switzerland: IUCN. x + 86pp.
- Dunbar, R. 1998. Impact of global warming on the distribution and survival of the gelada baboon: a modelling approach. *Global Change Biology* **4**:293-304.
- Edwards, M. S., and D. E. Ullrey. 1999. Effect of dietary fiber concentration on apparent digestibility and digesta passage in non - human primates. II. Hindgut - and foregut - fermenting folivores. *Zoo Biology* **18**:537-549.

- Estrada, A., P. A. Garber, A. B. Rylands, C. Roos, E. Fernandez-Duque, A. Di Fiore, K. A.-I. Nekaris, V. Nijman, E. W. Heymann, and J. E. Lambert. 2017. Impending extinction crisis of the world's primates: Why primates matter. *Science Advances* **3**:e1600946.
- Estrada, A., B. E. Raboy, and L. C. Oliveira. 2012. Agroecosystems and primate conservation in the tropics: a review. *American Journal of Primatology* **74**:696-711.
- Eudey, A. A. 2008. The crab-eating macaque (*Macaca fascicularis*): widespread and rapidly declining. *Primate Conservation* **23**:129-132.
- Fashing, P. J., E. S. Dierenfeld, and C. B. Mowry. 2007. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega Forest, Kenya. *International Journal of Primatology* **28**:673-703.
- Fedigan, L. M. 1990. Vertebrate predation in *Cebus capucinus*: meat eating in a neotropical monkey. *Folia primatologica* **54**:196-205.
- Fedigan, L. M., and M. J. Baxter. 1984. Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates* **25**:279-294.
- Fellowes, J. R., B. Chan, J. Zhou, S. Chen, S. Yang, and S. Ng. 2008. Current status of the Hainan gibbon (*Nomascus hainanus*): progress of population monitoring and other priority actions. *Asian Primates Journal* **1**:2-11.
- Felton, A. M., A. Felton, D. B. Lindenmayer, and W. J. Foley. 2009a. Nutritional goals of wild primates. *Functional Ecology* **23**:70-78.
- Felton, A. M., A. Felton, D. Raubenheimer, S. J. Simpson, W. J. Foley, J. T. Wood, I. R. Wallis, and D. B. Lindenmayer. 2009b. Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology* **20**:685-690.
- Felton, A. M., A. Felton, J. T. Wood, W. J. Foley, D. Raubenheimer, I. R. Wallis, and D. B. Lindenmayer. 2009c. Nutritional Ecology of *Ateles chamek* in lowland Bolivia: How Macronutrient Balancing Influences Food Choices. *International Journal of Primatology* **30**:675-696.
- Fiszman, S., and P. Varela. 2013. The satiating mechanisms of major food constituents—An aid to rational food design. *Trends in Food Science & Technology* **32**:43-50.
- Fitzpatrick, R., K. G. Abrantes, J. Seymour, and A. Barnett. 2011. Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behaviour? *Coral Reefs* **30**:569-577.
- Forthman-Quick, D., and M. Demment. 1988. Dynamics of exploitation: differential energetic adaptations of two troops of baboons to recent human contact. Pages 25-51 in Fa J. E. and Southwick C. H., editors. *Ecology and Behaviour of Food Enhanced Primate Groups*. A.R. Liss, USA.
- Freese, C. 1976. Censusing *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus* in the Costa Rican dry forest. Pages 4-9 in Heltne P. G., editor. *Neotropical primates: Field Studies and Conservation*. National Academy of Sciences, Washington DC.

- Fuller, M. F. 2004. The encyclopedia of farm animal nutrition. Cabi, Oxfordshire, U.K.
- Garber, P. A. 1993. Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology* **14**:145-166.
- Ghaly, A. E., and F. Alkoik. 2009. The yellow mealworm as a novel source of protein. *American Journal of Agricultural and Biological Sciences* **4**:319-331.
- Gonzalez-Zamora, A., V. Arroyo-Rodríguez, O. M. Chaves, S. Sánchez-López, K. E. Stoner, and P. Riba-Hernandez. 2009. Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. *American Journal of Primatology* **71**:8-20.
- González - Zamora, A., V. Arroyo - Rodríguez, Ó. M. Chaves, S. Sánchez - López, K. E. Stoner, and P. Riba - Hernández. 2009. Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. *American Journal of Primatology* **71**:8-20.
- Goodchild, S., and C. Schwitzer. 2008. The problem of obesity in captive lemurs. *International Zoo News* **55**:353-357.
- Gosby, A. K., A. D. Conigrave, D. Raubenheimer, and S. J. Simpson. 2013. Protein leverage and energy intake. *Obesity Research & Clinical Practice* **7**:e110.
- Green, R., and K. Higginbottom 2001. Negative effects of wildlife tourism on wildlife. CRC for Sustainable Tourism Gold Coast, Australia.
- Groves, C. P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, D.C.
- Grueter, C. C. 2013. *The Biology of Snub-nosed Monkeys, Douc Langurs, Proboscis Monkeys, and Simakobu*. Nova Biomedical, New York.
- Guillotin, M., G. Dubost, and D. Sabatier. 1994. Food choice and food competition among the three major primate species of French Guiana. *Journal of Zoology* **233**:551-579.
- Guo, S., B. Li, and K. Watanabe. 2007. Diet and activity budget of *Rhinopithecus roxellana* in the Qinling Mountains, China. *Primates* **48**:268-276.
- Hammerschlag, N., A. J. Gallagher, J. Wester, J. Luo, and J. S. Ault. 2012. Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Functional Ecology* **26**:567-576.
- Hanya, G., N. Noma, and N. Agetsuma. 2003. Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. *Primates* **44**:51-59.
- Heiduck, S. 1997. Food choice in masked titi monkeys (*Callicebus personatus melanochir*): selectivity or opportunism? *International Journal of Primatology* **18**:487-502.
- Hewson-Hughes, A. K., V. L. Hewson-Hughes, A. Colyer, A. T. Miller, S. J. McGrane, S. R. Hall, R. F. Butterwick, S. J. Simpson, and D. Raubenheimer. 2013. Geometric analysis of macronutrient selection in breeds of the domestic dog, *Canis lupus familiaris*. *Behavioral Ecology* **24**:293-304.

- Hewson-Hughes, A. K., V. L. Hewson-Hughes, A. T. Miller, S. R. Hall, S. J. Simpson, and D. Raubenheimer. 2011. Geometric analysis of macronutrient selection in the adult domestic cat, *Felis catus*. *Journal of Experimental Biology* **214**:1039-1051.
- Higginbottom, K. 2004. Wildlife tourism. *CRC for Sustainable Tourism* **1**:1-301.
- Hill, D. A. 1997. Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. *American Journal of Primatology* **43**:305-320.
- Hines, K. N. 2011. Effects of ecotourism on endangered northern Bahamian Rock Iguanas (*Cyclura cyclura*). *Herpetological Conservation and Biology* **6**:250-259.
- Hladik, C. M., and B. Simmen. 1996. Taste perception and feeding behavior in non-human primates and human populations. *Evolutionary Anthropology* **5**:58-71.
- Hsu, M. J., C. C. Kao, and G. Agoramorthy. 2009. Interactions between visitors and Formosan macaques (*Macaca cyclopis*) at Shou-Shan Nature Park, Taiwan. *American Journal of Primatology* **71**:214-222.
- Hu, J. 1998. *China Red Data Book of Endangered Animals: Mammalia*. Science Press, China.
- Huang, K., S. Guo, S. A. Cushman, D. W. Dunn, X. Qi, R. Hou, J. Zhang, Q. Li, Q. Zhang, and Z. Shi. 2016. Population structure of the golden snub-nosed monkey *Rhinopithecus roxellana* in the Qinling Mountains, central China. *Integrative Zoology* **11**:350-360.
- Irwin, M. T., J.-L. Raharison, D. R. Raubenheimer, C. A. Chapman, and J. M. Rothman. 2015. The nutritional geometry of resource scarcity: effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. *PloS One* **10**:e0128046.
- IUCN. The IUCN Red List of Threatened Species. Available from <http://www.iucnredlist.org/search> (accessed 2010-2015).
- Izawa, K. 1978. Frog-eating behavior of wild black-capped capuchin (*Cebus apella*). *Primates* **19**:633-642.
- Janson, C. H. 1990. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour* **40**:910-921.
- Johnson-Delaney, C. A. 2008. Nonhuman primate dental care. *Journal of Exotic Pet Medicine* **17**:138-143.
- Johnson, C. A., D. Raubenheimer, J. M. Rothman, D. Clarke, and L. Swedell. 2013. 30 days in the life: daily nutrient balancing in a wild chacma baboon. *PLoS One* **8**:e70383.
- Jones, C. G., W. Heck, R. E. Lewis, Y. Mungroo, G. Slade, and T. Cade. 1995. The restoration of the Mauritius kestrel *Falco punctatus* population. *Ibis* **137**:S173-S180.
- Jones, S., and D. Raubenheimer. 2001. Nutritional regulation in nymphs of the German cockroach, *Blattella germanica*. *Journal of Insect Physiology* **47**:1169-1180.
- Kay, R., P. Hoppe, and G. Maloiy. 1976. Fermentative digestion of food in the colobus monkey, *Colobus polykomos*. *Cellular and Molecular Life Sciences* **32**:485-487.

- Key, C., and C. Ross. 1999. Sex differences in energy expenditure in non-human primates. *Proceedings of the Royal Society of London B: Biological Sciences* **266**:2479-2485.
- Kinzey, W. G., and M. A. Norconk. 1990. Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology* **81**:5-15.
- Kirkpatrick, R. C., and C. C. Grueter. 2010. Snub-nosed monkeys: Multilevel societies across varied environments. *Evolutionary Anthropology: Issues, News, and Reviews* **19**:98-113.
- Kleiman, D. G. 1989. Reintroduction of Captive Mammals for Conservation. *BioScience* **39**:152-161.
- Kleiman, D. G., B. B. Beck, J. M. Dietz, L. A. Dietz, J. D. Ballou, and A. F. Coimbra-Filho. 1986. Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies, and reintroduction. Pages 959-979 in Benirschke K., editor. *Primates - The Road to Self-Sustaining Populations*. Springer, New York.
- Knapp, C. R., K. N. Hines, T. T. Zachariah, C. Perez-Heydrich, J. B. Iverson, S. D. Buckner, S. C. Halach, C. R. Lattin, and L. M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. *Conservation Physiology* **1**:cot032.
- Kool, K. 1992. Food selection by the silver leaf monkey, *Trachypithecus auratus sondaicus*, in relation to plant chemistry. *Oecologia* **90**:527-533.
- Kurita, H., Y. Sugiyama, H. Ohsawa, Y. Hamada, and T. Watanabe. 2008. Changes in demographic parameters of *Macaca fuscata* at Takasakiyama in relation to decrease of provisioned foods. *International Journal of Primatology* **29**:1189-1202.
- Kurland, J. A., and S. J. Gaulin. 1987. Comparability among measures of primate diets. *Primates* **28**:71-77.
- Laidlaw, R. 1998. Virgin Jungle Reserves of Peninsular Malaysia: small protected areas in logged forest. *The Commonwealth Forestry Review*:83-90.
- Lambert, J. E., and J. M. Rothman. 2015. Fallback foods, optimal diets, and nutritional targets: Primate responses to varying food availability and quality. *Annual Review of Anthropology* **44**:493-512.
- Laska, M. 1996. Taste preference thresholds for food-associated sugars in the squirrel monkey (*Saimiri sciureus*). *Primates* **37**:91-95.
- Laska, M., L. T. H. Salazar, and E. R. Luna. 2000. Food preferences and nutrient composition in captive spider monkeys, *Ateles geoffroyi*. *International Journal of Primatology* **21**:671-683.
- Laska, M., E. C. Sanchez, and E. R. Luna. 1998. Relative taste preferences for food-associated sugars in the spider monkey (*Ateles geoffroyi*). *Primates* **39**:91-96.

- Laska, M., E. Schüll, and H.P. Scheuber. 1999. Taste preference thresholds for food-associated sugars in baboons (*Papio hamadryas anubis*). *International Journal of Primatology* **20**:25-34.
- Lawler, I. R., Aragonés, L., Berding, N., Marsh, H., and Foley, W. J. 2006. Near infrared spectroscopy is a rapid, cost-effective predictor of seagrass nutrients. *Journal of Chemical Ecology* **32**:1353–1365.
- Lee, K. P., S. J. Simpson, F. J. Clissold, R. Brooks, J. W. O. Ballard, P. W. Taylor, N. Soran, and D. Raubenheimer. 2008. Lifespan and reproduction in *Drosophila*: new insights from nutritional geometry. *Proceedings of the National Academy of Sciences* **105**:2498-2503.
- Leighton, M. 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* **14**:257-313.
- Li, B., C. Chen, W. Ji, and B. Ren. 2000. Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Folia Primatologica* **71**:375-386.
- Li, B., H. Li, D. Zhao, Y. Zhang, and X. Qi. 2005. Study on dominance hierarchy of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Qinling Mountains. *Acta Theriologica Sinica* **26**:18-25.
- Li, H., S.-J. Meng, Z.-M. Men, Y.-X. Fu, and Y.-P. Zhang. 2003. Genetic diversity and population history of golden monkeys (*Rhinopithecus roxellana*). *Genetics* **164**:269-275.
- Li, Y. 2006. Seasonal variation of diet and food availability in a group of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China. *American Journal of Primatology* **68**:217-233.
- Li, Y. 2007. Terrestriality and tree stratum use in a group of Sichuan snub-nosed monkeys. *Primates* **48**:197-207.
- Li, Y., Z. Jiang, C. Li, and C. C. Grueter. 2010. Effects of Seasonal Folivory and Frugivory on Ranging Patterns in *Rhinopithecus roxellana*. *International Journal of Primatology* **31**:609-626.
- Li, Y., C. B. Stanford, and Y. Yuhui. 2002. Winter feeding tree choice in Sichuan snub-nosed monkeys (*Rhinopithecus roxellanae*) in Shennongjia Nature Reserve, China. *International Journal of Primatology* **23**:657-675.
- Linder, J. M., and J. F. Oates. 2011. Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biological Conservation* **144**:738-745.
- Liu, X., C. B. Stanford, J. Yang, H. Yao, and Y. Li. 2013. Foods eaten by the Sichuan Snub-nosed Monkey (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve,

- China, in relation to nutritional chemistry. *American Journal of Primatology* **75**:860-871.
- Marks, D. L., T. Swain, S. Goldstein, A. Richard, and M. Leighton. 1988. Chemical correlates of rhesus monkey food choice: The influence of hydrolyzable tannins. *Journal of Chemical Ecology* **14**:213-235.
- Martinez-Cordero, C., C. W. Kuzawa, D. M. Sloboda, J. Stewart, S. J. Simpson, and D. Raubenheimer. 2012. Testing the Protein Leverage Hypothesis in a free-living human population. *Appetite* **59**:312-315.
- Masette, M., G. Isabirye - Basuta, D. Baranga, C. A. Chapman, and J. M. Rothman. 2015. The challenge of interpreting primate diets: mangabey foraging on *Blighia unijugata* fruit in relation to changing nutrient content. *African Journal of Ecology* **53**:259-267.
- Mathy, J., and L. Isbell. 2001. The Relative Importance of Size of Food and Interfood Distance in Eliciting Aggression in Captive Rhesus Macaques. *Folia Primatologica* **72**:268-277.
- Maynard, A. B., and Loosli, J. K. 1969. *Animal Nutrition*. McGraw-Hill, New York.
- McCabe, G. M., and L. M. Fedigan. 2007. Effects of Reproductive Status on Energy Intake, Ingestion Rates, and Dietary Composition of Female *Cebus capucinus* at Santa Rosa, Costa Rica. *International Journal of Primatology* **28**:837-851.
- McCarthy, M. S., M. D. Matheson, J. D. Lester, L. K. Sheeran, J.-H. Li, and R. S. Wagner. 2009. Sequences of Tibetan Macaque (*Macaca thibetana*) and Tourist Behaviors at Mt. Huangshan, China. *Primate Conservation* **24**:145-151.
- McConkey, K. R., A. Ario, F. Aldy, and D. J. Chivers. 2003. Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, Central Kalimantan. *International Journal of Primatology* **24**:19-32.
- McKey, D. B., J. S. Gartlan, P. G. Waterman, and G. M. Choo. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biological Journal of the Linnean Society* **16**:115-146.
- McLennan, M. R. 2013. Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest–farm interface. *International Journal of Primatology* **34**:585-614.
- Méndez-Carvajal, P. G. 2013. Population size, distribution and conservation status of howler monkeys (*Alouatta coibensis trabeata*) and spider monkeys (*Ateles geoffroyi azuerensis*) on the Azuero Peninsula, Panama. *Primate Conservation* **26**:3-15.
- Miller, J. R., and R. J. Hobbs. 2007. Habitat restoration—do we know what we’re doing? *Restoration Ecology* **15**:382-390.
- Milner-Gulland, E. J., and E. L. Bennett. 2003. Wild meat: the bigger picture. *Trends in Ecology & Evolution* **18**:351-357.
- Milton, K. 1981. Food choice and digestive strategies of two sympatric primate species. *The American Naturalist* **117**:496-505.

- Milton, K. 1999. Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition* **15**:488-498.
- Milton, K. 2008. Macronutrient patterns of 19 species of Panamanian fruits from Barro Colorado Island. *Neotropical Primates* **15**:1-7.
- Mittermeier, R. A., Boubli, J.-P. & Di Fiore, A. 2008a. *Ateles marginatus*. The IUCN Red List of Threatened Species 2008. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T2282A9390334.en>.
- Mittermeier, R. A., Rylands, A.B. & Boubli, J.-P. 2008b. *Ateles paniscus*. The IUCN Red List of Threatened Species 2008. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T2283A9392691.en>.
- Moran, J. 2005. Tropical dairy farming: feeding management for small holder dairy farmers in the humid tropics. Csiro Publishing, Australia.
- Mowry, C. B., B. S. Decker, and D. J. Shure. 1996. The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Procolobus badius rufomitatus*). *International Journal of Primatology* **17**:63-84.
- Murray, C. M., E. V. Lonsdorf, L. E. Eberly, and A. E. Pusey. 2009. Reproductive energetics in free-living female chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology*:arp114.
- Murray, M. H., D. J. Becker, R. J. Hall, and S. M. Hernandez. 2016. Wildlife health and supplemental feeding: A review and management recommendations. *Biological Conservation* **204** (Part B):163-174.
- Nagy, K. A. 2005. Field metabolic rate and body size. *Journal of Experimental Biology* **208**:1621-1625.
- National Research Council. 1989. Recommended Dietary Allowances. The National Academies Press, Washington, DC.
- National Research Council. 2003. Nutrient Requirements of Nonhuman Primates: Second Revised Edition. The National Academies Press, Washington, DC.
- Naughton-Treves, L., A. Treves, C. Chapman, and R. Wrangham. 1998. Temporal patterns of crop - raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology* **35**:596-606.
- Newsome, D., and K. Rodger. 2013. Feeding of wildlife: an acceptable practice in ecotourism? Page 436 in Ballantyne R., and Packer J., editors. *International Handbook on Ecotourism*. Edward Elgar Publishing, U.K.
- Nie, Y., Z. Zhang, D. Raubenheimer, J. J. Elser, W. Wei, and F. Wei. 2015. Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. *Functional Ecology* **29**:26-34.
- Nijboer, J. 2006. The digestive physiology of colobine primates. Fibre Intake and Faeces Quality in Leaf-eating Primates. (Doctoral dissertation, Utrecht University).

- Nijman, V., K. Nekaris, G. Donati, M. Bruford, and J. Fa. 2011. Primate conservation: measuring and mitigating trade in primates. *Endangered Species Research* **13**:159-161.
- O'Leary, H. 1996. Contrasts in diet amongst barbary macaques on Gibraltar: human influences. *Animal Welfare* **5**:177-188.
- O'Mara, M. T., and C. M. Hickey. 2014. The development of sex differences in ring-tailed lemur feeding ecology. *Behavioral Ecology and Sociobiology* **68**:1273-1286.
- Oates, J. F. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology* **21**:1-9.
- Oates, J. F., P. G. Waterman, and G. M. Choo. 1980. Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* **45**:45-56.
- Orams, M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management* **23**:281-293.
- Otoni, E. B., and M. Mannu. 2001. Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *International Journal of Primatology* **22**:347-358.
- Ozoga, J. J., and L. J. Verme. 1982. Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. *The Journal of Wildlife Management*:281-301.
- Pan, D., Y. Li, H. Hu, S. Meng, Z. Men, Y. Fu, and Y. Zhang. 2005. Microsatellite polymorphisms of Sichuan golden monkeys. *Chinese Science Bulletin* **50**:2850.
- Picciano, M. F. 2003. Pregnancy and lactation: physiological adjustments, nutritional requirements and the role of dietary supplements. *The Journal of Nutrition* **133**:1997S-2002S.
- Plowman, A. 2013. Diet review and change for monkeys at Paignton Zoo Environmental Park. *Journal of Zoo and Aquarium Research* **1**:73-77.
- Popkin, B. M., L. S. Adair, and S. W. Ng. 2012. Global nutrition transition and the pandemic of obesity in developing countries. *Nutrition Reviews* **70**:3-21.
- Potter, J. S., and M. Clauss. 2005. Mortality of captive giraffe (*Giraffa camelopardalis*) associated with serous fat atrophy: a review of five cases at Auckland Zoo. *Journal of Zoo and Wildlife Medicine* **36**:301-307.
- Putnam, P., C. Elam, R. Davis, and J. Wiltbank. 1966. Dietary energy and protein effects on rumen volatile acids and ration digestibility by beef heifers. *Journal of Animal Science* **25**:988-993.
- Qi, X.-G., P. A. Garber, W. Ji, Z.-P. Huang, K. Huang, P. Zhang, S.-T. Guo, X.-W. Wang, G. He, and P. Zhang. 2014. Satellite telemetry and social modeling offer new insights into the origin of primate multilevel societies. *Nature Communications* **5**.
- Qi, X. G., B. G. Li, and W. H. Ji. 2008. Reproductive parameters of wild female *Rhinopithecus roxellana*. *American Journal of Primatology* **70**:311-319.

- Racela Jr, A., H. Grady, J. Higginson, and D. Svoboda. 1966. Protein deficiency in rhesus monkeys. *The American Journal of Pathology* **49**:419.
- Ramos-Fernández, G., and B. Ayala-Orozco. 2003. Population size and habitat use of spider monkeys at Punta Laguna, Mexico. Pages 191-209 in Marsh L. K., editor. *Primates in Fragments*. Springer, New York.
- Raubenheimer, D. 2011. Toward a quantitative nutritional ecology: the right-angled mixture triangle. *Ecological Monographs* **81**:407-427.
- Raubenheimer, D., and S. A. Jones. 2006. Nutritional imbalance in an extreme generalist omnivore: tolerance and recovery through complementary food selection. *Animal Behaviour* **71**:1253-1262.
- Raubenheimer, D., G. E. Machovsky-Capuska, A. K. Gosby, and S. Simpson. 2015. Nutritional ecology of obesity: from humans to companion animals. *British Journal of Nutrition* **113**:S26-S39.
- Raubenheimer, D., and S. J. Simpson. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews* **10**:151-179.
- Raubenheimer, D., S. J. Simpson, and D. Mayntz. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology* **23**:4-16.
- Raubenheimer, D., S. J. Simpson, and A. H. Tait. 2012. Match and mismatch: conservation physiology, nutritional ecology and the timescales of biological adaptation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **367**:1628-1646.
- Remis, M., and M. Kerr. 2002. Taste responses to fructose and tannic acid among gorillas (*Gorilla gorilla gorilla*). *International Journal of Primatology* **23**:251-261.
- Remis, M. J. 2003. Are gorillas vacuum cleaners of the forest floor? The roles of body size, habitat, and food preferences on dietary flexibility and nutrition. Pages 385-404 in Taylor A. B., and Goldsmith M. L., editors. *Gorilla biology: A Multidisciplinary Perspective*. Cambridge University Press.
- Rennei, R., R. C. Kirkpatrick, N. G. Jablonski, W. V. Bleisch, and X. C. Le. 1998. Conservation status and prospects of the snub-nosed langurs (*Colobinae: Rhinopithecus*). Pages 301-314 in Jablonski N. G., editor. *The Natural History of the Doucs and Snub-nosed monkeys*. World Scientific Publishing, Singapore.
- Reynolds, P. C., and D. Braithwaite. 2001. Towards a conceptual framework for wildlife tourism. *Tourism Management* **22**:31-42.
- Riley, E. P., B. Tolbert, and W. R. Farida. 2013. Nutritional content explains the attractiveness of cacao to crop raiding Tonkean macaques. *Current Zoology* **59**:160-169.
- Robinson, J. G. 1981. Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Animal Behaviour* **29**:1036-1056.

- Roos, C., R. Boonratana, J. Supriatna, J. R. Fellowes, A. B. Rylands, and R. A. Mittermeier. 2013. An updated taxonomy of primates in Vietnam, Laos, Cambodia and China. *Vietnamese Journal of Primatology* **2**:13-26.
- Rose, L. M. 1994. Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology* **15**:95-114.
- Ross, C. 2001. Park or ride? Evolution of infant carrying in primates. *International Journal of Primatology* **22**:749-771.
- Rothman, J. M., C. A. Chapman, and A. N. Pell. 2008a. Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. *American Journal of Primatology* **70**:690-694.
- Rothman, J. M., C. A. Chapman, and P. J. Van Soest. 2011a. Methods in Primate Nutritional Ecology: A User's Guide. *International Journal of Primatology* **33**:542-566.
- Rothman, J. M., C. A. Chapman, and P. J. Van Soest. 2012. Methods in primate nutritional ecology: a user's guide. *International Journal of Primatology* **33**:542-566.
- Rothman, J. M., E. S. Dierenfeld, H. F. Hintz, and A. N. Pell. 2008b. Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia* **155**:111-122.
- Rothman, J. M., D. Raubenheimer, and C. A. Chapman. 2011b. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biology Letters* **7**:847-849.
- Ryder, O. A., and A. T. Feistner. 1995. Research in zoos: a growth area in conservation. *Biodiversity & Conservation* **4**:671-677.
- Rylands, A. B., C. P. Groves, R. A. Mittermeier, L. Cortés-Ortiz, and J. J. Hines. 2006. Taxonomy and distributions of Mesoamerican primates. Pages 29-79 in Estrada A., Garber P. A., Pavelka M. S. M., and Luecke L., editors. *New Perspectives in the Study of Mesoamerican Primates*. Springer, USA.
- Saj, T., P. Sicotte, and J. D. Paterson. 1999. Influence of human food consumption on the time budget of vervets. *International Journal of Primatology* **20**:977-994.
- Schmidt, D. A., M. S. Kerley, J. H. Porter, and J. L. Dempsey. 2005. Structural and nonstructural carbohydrate, fat, and protein composition of commercially available, whole produce. *Zoo Biology* **24**:359-373.
- Schoech, S. J., E. S. Bridge, R. K. Boughton, S. J. Reynolds, J. W. Atwell, and R. Bowman. 2008. Food supplementation: a tool to increase reproductive output? A case study in the threatened Florida Scrub-Jay. *Biological Conservation* **141**:162-173.
- Schwitzer, C., and W. Kaumanns. 2001. Body weights of ruffed lemurs (*Varecia variegata*) in European zoos with reference to the problem of obesity. *Zoo Biology* **20**:261-269.
- Schwitzer, C., R. Mittermeier, A. Rylands, L. Taylor, F. Chiozza, E. Williamson, J. Wallis, and F. Clark. 2014. Primates in peril: The world's 25 most endangered primates 2012–2014. IUCN SSC Primate Specialist Group (PSG), International Primatological Society (IPS),

- Conservation International (CI), and Bristol Zoological Society, Arlington, VA. iv+93pp.
- Schwitzer, C., S. Polowinsky, and C. Solman. 2009. Fruits as foods—common misconceptions about frugivory. *Zoo Animal Nutrition IV*. Fürth: Filander Verlag:131-168.
- Simmen, B., and C. M. Hladik. 1998. Sweet and bitter taste discrimination in primates: scaling effects across species. *Folia Primatologica* **69**:129-138.
- Simmen, B., and D. Sabatier. 1996. Diets of some French Guianan primates: food composition and food choices. *International Journal of Primatology* **17**:661-693.
- Simpson, S., and D. Raubenheimer. 1995. The geometric analysis of feeding and nutrition: a user's guide. *Journal of Insect Physiology* **41**:545-553.
- Simpson, S. J., and D. Raubenheimer 2012. *The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity*. Princeton University Press, Princeton, NJ.
- Slater, K. Y., C. M. Schaffner, and F. Aureli. 2009. Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of Primatology* **71**:21-29.
- Smith, B. L. 2001. Winter feeding of elk in western North America. *The Journal of Wildlife Management*:173-190.
- Smokorowski, K., K. Withers, and J. Kelso. 1998. Does habitat creation contribute to management goals? An evaluation of literature documenting freshwater habitat rehabilitation or enhancement projects. *Canadian Technical Report of Fisheries and Aquatic Sciences No. 2249*.
- Strier, K. B. 2000. *Primate Behavioral Ecology*. Allyn and Bacon, Boston.
- Stubbs, R. J., D. A. Hughes, A. M. Johnstone, G. W. Horgan, N. King, and J. E. Blundell. 2004. A decrease in physical activity affects appetite, energy, and nutrient balance in lean men feeding ad libitum. *The American Journal of Clinical Nutrition* **79**:62-69.
- Suarez, S. A. 2006. Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. *International Journal of Primatology* **27**:411-436.
- Sullivan, J. 1966. Studies of the hemicelluloses of forage plants. *Journal of Animal Science* **25**:83-86.
- Tan, C. L., S. Guo, and B. Li. 2007. Population Structure and Ranging Patterns of *Rhinopithecus roxellana* in Zhouzhi National Nature Reserve, Shaanxi, China. *International Journal of Primatology* **28**:577-591.
- Tobey, J., C. Andrus, L. Doyle, V. Thompson, and F. Bercovitch. 2006. Maternal effort and joey growth in koalas (*Phascolarctos cinereus*). *Journal of Zoology* **268**:423-431.
- Townsend, D. E., R. L. Lochmiller, S. J. DeMaso, D. M. Leslie Jr, A. D. Peoples, S. A. Cox, and E. S. Parry. 1999. Using supplemental food and its influence on survival of northern bobwhite (*Colinus virginianus*). *Wildlife Society Bulletin*:1074-1081.

- Tsuji, Y., G. Hanya, and C. C. Grueter. 2013. Feeding strategies of primates in temperate and alpine forests: comparison of Asian macaques and colobines. *Primates* **54**:201-215.
- Urbani, B., Morales, A. L., Link, A. & Stevenson, P. 2008. *Ateles hybridus*. The IUCN Red List of Threatened Species 2008. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T39961A10280054.en>.
- van Huis, A., J. van Itterbeeck, H. Klunder, E. Mertens, A. Halloran, G. Muir, and P. Vantomme. 2013. Nutritional Value of Insects for Human Consumption. Pages 67-88. *Edible Insects : Future Prospects for Food and Feed Security*. FAO, Rome.
- van Schaik, C. P., and A. Maria. 1986. The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour* **99**:296-314.
- van Soest, P. J. 1982. *Nutritional Ecology of the Ruminant*. Cornell University Press, New York.
- van Soest, P. J. 1994. *Nutritional Ecology of the Ruminant*. Cornell University Press, Ithaca, New York.
- van Soest, P. v., J. Robertson, and B. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**:3583-3597.
- Vermeer, J. 1994. Notes on the management of the woolly monkey in captivity. *International Zoo News* **255**:8-13.
- Vignon, M., P. Sasal, R. L. Johnson, and R. Galzin. 2010. Impact of shark-feeding tourism on surrounding fish populations off Moorea Island (French Polynesia). *Marine and Freshwater Research* **61**:163-169.
- Wallace, R. B., Mittermeier, R.A., Cornejo, F. & Boubli, J.-P. 2008. *Ateles chamek*. The IUCN Red List of Threatened Species 2008. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41547A10497375.en>
- Walpole, M. J. 2001. Feeding dragons in Komodo National Park: a tourism tool with conservation complications. *Animal Conservation* **4**:67-73.
- Washburn, S. L. 1981. Longevity in primates. Pages 11-29 in McGaugh J. L. and Kiesler S. B., editors. *Aging: Biology and Behavior*. Academic Press, New York.
- Waterman, P. G. 1984. Food acquisition and processing as a function of plant chemistry. Pages 177-211 in Chivers D. J., Wood B. A., and Bilsborough A., editors. *Food Acquisition and Processing in Primates*. Springer, USA.
- Waterman, P. G., J. A. Ross, E. L. Bennett, and A. Davies. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biological Journal of the Linnean Society* **34**:1-32.

- Xiang, Z., Y. Yu, M. Yang, J. Yang, M. Niao, and M. Li. 2011. Does flagship species tourism benefit conservation? A case study of the golden snub-nosed monkey in Shennongjia National Nature Reserve. *Chinese Science Bulletin* **56**:2553-2558.
- Yamagiwa, J., and A. K. Basabose. 2006. Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi-Biega National Park. *Primates* **47**:74-90.
- Yang, B., P. Zhang, P. A. Garber, R. Hedley, and B. Li. 2016. Sichuan Snub-Nosed Monkeys (*Rhinopithecus roxellana*) Consume Cicadas in the Qinling Mountains, China. *Folia Primatologica* **87**:11-16.
- Yao, H., X. Liu, C. Stanford, J. Yang, T. Huang, F. Wu, and Y. Li. 2011. Male dispersal in a provisioned multilevel group of *Rhinopithecus roxellana* in Shennongjia Nature Reserve, China. *American Journal of Primatology* **73**:1280-1288.
- Yiming, L. 2006. Seasonal variation of diet and food availability in a group of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China. *American Journal of Primatology* **68**:217-233.
- Yingxiang, W., J. Xuelong, and L. Dewu. 1998. Classification and Distribution of the Extant Subspecies of Golden Snub-nosed Monkey (*Rhinopithecus* [*Rhinopithecus*] *roxellana*). Pages 53-64 in Jablonski N. G., editor. *The Natural History of the Doucs and Snub-nosed monkeys*. World Scientific Publishing, Singapore.
- Yongcheng, L. R., M. 2008. *Rhinopithecus roxellana*. The IUCN Red List of Threatened Species. Available from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T19596A8985735.en>.
- Zhang, P., K. Watanabe, and B. Li. 2008a. Female social dynamics in a provisioned free-ranging band of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains, China. *American Journal of Primatology* **70**:1013-1022.
- Zhang, P., K. Watanabe, B. Li, and X. Qi. 2008b. Dominance relationships among one-male units in a provisioned free-ranging band of the Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, China. *American Journal of Primatology* **70**:634-641.
- Zhang, P., K. Watanabe, B. Li, and C. L. Tan. 2006a. Social organization of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, Central China. *Primates* **47**:374-382.
- Zhang, P., K. Watanabe, B. Li, and C. L. Tan. 2006b. Social organization of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, Central China. *Primates* **47**:374-382.
- Zhang, S., B. Ren, and B. Li. 1999. A juvenile Sichuan golden monkey (*Rhinopithecus roxellana*) predated by a goshawk (*Accipiter gentilis*) in the Qinling Mountains. *Folia Primatologica* **70**:175-176.

- Zhao, D., W. Ji, B. Li, and K. Watanabe. 2008. Mate competition and reproductive correlates of female dispersal in a polygynous primate species (*Rhinopithecus roxellana*). *Behavioural Processes* **79**:165-170.
- Zhao, D., and B. Li. 2009. 23 Years Research of Sichuan Snub-Nosed Monkeys (*Rhinopithecus roxellana*) in Zhouzhi National Nature Reserve, China. *Asian Primates Journal* **1**:19-23.
- Zhao, D., Wang, X., Watanabe, K., Li, B. 2008. Eurasian blackbird predated by wild *Rhinopithecus roxellana* in the Qinling Mountains, China. *Integrative Zoology* **3**:176-179.
- Zhou, Q., F. Wei, M. Li, C. Huang, and B. Luo. 2006. Diet and Food Choice of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. *International Journal of Primatology* **27**:1441-1460.

Appendix 1

Table A1.1. The proportional nutritional composition of foods consumed by the troop during summer and autumn. Foods are sorted by their contribution to the troop's diet (by weight). Local names have been used for unidentifiable species. UI=unidentifiable by Latin name or local name.

Species	Part	%CP	%Lipids	%NSC	%NDF	%Lignin	Proportion of Diet	Season
<i>Morus alba</i>	leaves	30.4%	6.5%	17.5%	42.3%	3.3%	36.5%	Late Summer
<i>Morus alba</i>	leaves	27.0%	3.3%	15.8%	41.9%	11.9%	36.5%	Early Summer
<i>Morus alba</i>	leaves	20.7%	2.2%	25.1%	36.0%	16.0%	27.4%	Autumn
<i>Litsea rubescens</i>	fruit	12.5%	22.2%	13.8%	35.0%	16.6%	18.0%	Summer
<i>Quercus aliena</i>	seeds	4.4%	0.9%	54.4%	38.9%	1.5%	16.3%	Autumn
<i>Cornus spp</i>	fruit	12.2%	7.0%	11.4%	49.6%	19.8%	13.5%	Summer
<i>Pinus massoniana</i>	seeds	3.7%	8.0%	8.1%	60.7%	19.5%	11.4%	Autumn
<i>Lindera obtusiloba</i>	fruit	8.4%	34.4%	9.7%	28.1%	19.5%	9.8%	Summer
<i>Crataegus cuneata</i>	fruit	4.1%	7.9%	27.9%	45.2%	14.9%	8.4%	Summer
<i>Prunus armeniaca</i>	leaves	17.1%	6.4%	24.6%	49.3%	2.6%	7.8%	Autumn

Species	Part	%CP	%Lipids	%NSC	%NDF	%Lignin	Proportion of Diet	Season
Unidentified Fungus	fruiting body	12.7%	1.0%	20.0%	57.3%	9.1%	5.8%	Autumn
<i>Actinidia eriantha</i>	leaves	9.6%	1.9%	17.1%	36.0%	35.4%	4.5%	Autumn
<i>Glechoma longituba</i>	leaves	27.2%	3.4%	18.2%	42.3%	9.0%	4.4%	Autumn
<i>Malus baccata</i>	fruit	5.1%	2.1%	20.1%	44.7%	28.0%	4.1%	Autumn
<i>Grewia biloba</i>	leaves	19.8%	5.0%	10.9%	53.6%	10.7%	3.7%	Summer
<i>Grewia biloba</i>	leaves	22.5%	3.6%	16.6%	42.1%	15.1%	3.5%	Autumn
<i>Ulmus bergmanniana</i>	leaves	16.6%	2.9%	19.2%	47.9%	13.3%	2.6%	Autumn
<i>Prunus salicina</i>	leaves	23.3%	3.7%	14.5%	43.0%	15.5%	2.3%	Summer
<i>Qing Lian Zhi</i>	leaves	46.6%	4.2%	11.3%	31.5%	6.4%	1.6%	Summer
<i>Deutzia vilmorinae</i>	leaves	10.7%	6.0%	27.6%	43.5%	12.2%	1.6%	Autumn
<i>Celastrus orbiculatus</i>	fruit	11.5%	18.4%	20.8%	39.5%	9.9%	1.0%	Autumn
UI-1	leaves	23.7%	1.9%	28.4%	42.4%	3.6%	1.0%	Autumn
<i>Ulmus macrocarpa</i>	leaves	17.6%	1.8%	25.6%	45.8%	9.3%	0.9%	Autumn
<i>Celastrus orbiculatus</i>	fruit	13.1%	11.1%	15.3%	47.4%	13.1%	0.9%	Summer
<i>Schisandra chinensis</i>	leaves	14.7%	3.8%	16.1%	45.2%	20.2%	0.7%	Autumn

Species	Part	%CP	%Lipids	%NSC	%NDF	%Lignin	Proportion of Diet	Season
<i>Fraxinus mandshurica</i>	bark	7.8%	1.1%	35.3%	46.0%	9.8%	0.7%	Autumn
<i>Padus asiatica</i>	leaves	18.3%	3.7%	20.4%	46.5%	11.0%	0.7%	Late Summer
<i>Padus asiatica</i>	leaves	19.3%	5.0%	11.9%	42.2%	21.7%	0.7%	Early Summer
<i>Prunus pleiocerasus</i>	leaves	14.7%	2.7%	14.8%	53.2%	14.6%	0.7%	Summer
<i>Prunus salicina</i>	leaves	11.2%	3.8%	24.4%	49.1%	11.5%	0.6%	Autumn
<i>Padus asiatica</i>	bark	4.1%	2.0%	16.7%	54.4%	22.7%	0.6%	Autumn
<i>Acer mono</i>	bark	6.9%	1.7%	20.9%	57.9%	12.7%	0.6%	Autumn
<i>Meliosma cuneifolia</i>	leaves	12.3%	3.2%	11.6%	56.1%	16.9%	0.5%	Late Summer
<i>Meliosma cuneifolia</i>	leaves	14.0%	2.1%	10.3%	51.0%	22.7%	0.5%	Early Summer
UI-3	leaves	18.8%	2.2%	22.0%	47.8%	9.2%	0.5%	Autumn
<i>Ma Huan Shao</i>	seeds	21.4%	4.7%	12.7%	44.5%	16.7%	0.4%	Autumn
<i>Salix matsudana</i>	leaves	25.5%	4.4%	11.1%	51.9%	7.1%	0.4%	Summer
<i>Padus spp</i>	leaves	13.3%	1.8%	23.9%	43.0%	18.0%	0.4%	Autumn
<i>Qing Gang Mu</i>	leaves	13.8%	2.8%	16.6%	47.1%	19.7%	0.4%	Autumn

Species	Part	%CP	%Lipids	%NSC	%NDF	%Lignin	Proportion of Diet	Season
<i>Toxicodendron vernicifluum</i>	leaves	18.0%	3.4%	21.0%	41.0%	16.6%	0.4%	Autumn
<i>Swida macrophylla</i>	leaves	14.8%	3.4%	23.6%	37.3%	21.0%	0.3%	Autumn
<i>Corylus heterophylla</i>	seeds	5.1%	7.6%	9.1%	50.4%	27.7%	0.3%	Autumn
<i>Prunus armeniaca</i>	leaves	22.5%	7.8%	15.8%	47.2%	6.8%	0.3%	Summer
<i>Qing Liang Zi</i>	leaves	14.3%	4.3%	33.2%	36.9%	11.3%	0.3%	Autumn
<i>Corylus ferox</i>	leaves	12.8%	5.1%	16.4%	46.1%	19.5%	0.3%	Summer
<i>Corylus heterophylla</i>	leaves	12.3%	4.9%	13.9%	51.7%	17.2%	0.3%	Summer
<i>Ji liu</i>	leaves	17.1%	1.7%	11.1%	51.1%	19.1%	0.3%	Summer
<i>Stachyurus chinensis</i>	leaves	26.5%	4.3%	14.9%	45.6%	8.7%	0.3%	Summer
<i>Actinidia eriantha</i>	leaves	14.3%	4.3%	33.2%	36.9%	11.3%	0.3%	Summer
<i>Padus asiatica</i>	fruit	20.1%	5.5%	23.1%	41.9%	9.5%	0.2%	Summer
<i>Ma Huan Shao</i>	leaves	15.1%	1.6%	13.3%	48.1%	21.9%	0.2%	Autumn
UI-1	bark	5.6%	7.4%	8.5%	52.3%	26.1%	0.2%	Summer
<i>Corylus chinensis</i>	leaves	13.3%	3.9%	13.9%	54.5%	14.4%	0.2%	Summer

Species	Part	%CP	%Lipids	%NSC	%NDF	%Lignin	Proportion of Diet	Season
<i>Ulmus macrocarpa</i>	leaves	13.7%	3.0%	19.2%	51.8%	12.3%	0.2%	Summer
<i>Salix matsudana</i>	leaves	13.4%	4.3%	17.5%	50.2%	14.6%	0.2%	Autumn
<i>Ku Dong Po</i>	leaves	16.2%	2.5%	21.0%	53.2%	7.2%	0.2%	Autumn
<i>Padus asiatica</i>	leaves	13.9%	2.9%	19.4%	41.7%	22.1%	0.2%	Autumn
UI-2	leaves	26.4%	2.7%	16.2%	46.3%	8.4%	0.2%	Summer
<i>Litsea rubescens</i>	leaves	12.7%	4.0%	23.2%	38.8%	21.2%	0.2%	Autumn
<i>Deutzia vilmorinae</i>	leaves	16.0%	2.5%	13.9%	40.3%	27.4%	0.2%	Summer
UI-2	bark	6.6%	1.9%	23.7%	62.3%	5.5%	0.1%	Autumn
<i>Grewia biloba</i>	bark	8.3%	1.5%	10.3%	52.8%	27.1%	0.1%	Autumn
<i>Salix spp</i>	leaves	14.1%	4.9%	21.1%	43.7%	16.2%	0.1%	Autumn
<i>Actinidia eriantha</i>	bark	8.2%	1.6%	22.1%	47.0%	21.0%	0.1%	Autumn
<i>Corylus heterophylla</i>	leaves	10.7%	1.8%	14.5%	54.8%	18.3%	0.0%	Autumn
<i>Huang Bo</i>	fruit	10.3%	4.6%	19.0%	58.2%	8.0%	0.0%	Autumn
<i>Lindera obtusiloba</i>	leaves	12.0%	1.2%	20.9%	39.4%	26.5%	0.0%	Summer
<i>Quercus aliena</i>	leaves	13.5%	4.5%	9.9%	56.6%	15.5%	0.0%	Summer

Table A1.2. The percentage of observations in which monkeys consumed different food

species during summer (top) and autumn (bottom). NLF=non-lactating female, LF=lactating

female, AM=adult male, J=juvenile. Local name used for plants that were unidentifiable.

Numbers in parentheses = number of observations in summer (June to August, 2011)/autumn

(October, 2012). B=bark, F=fruit, FB=fruiting body, L=leaves, S=Seeds.

Family	Food Species	NLF (62/30)	LF (71/28)	AM (71/36)	J (162/48)
<i>Aceraceae</i>	<i>Acer mono</i>	0%	0%	0%	0%
		0%	0%	3% (B)	2% (B)
<i>Actinidiaceae</i>	<i>Actinidia eriantha</i>	0%	1% (L)	0%	1% (L)
		0%	8% (B, L)	0%	0%
<i>Anacardiaceae</i>	<i>Toxicodendron vernicifluum</i>	0%	0%	0%	0%
		4% (L)	0%	0%	0%
<i>Betulaceae</i>	<i>Corylus chinensis</i>	3% (L)	0%	0%	1% (L)
		0%	0%	0%	0%
	<i>Corylus ferox</i>	0%	1% (L)	0%	0%
		0%	0%	0%	0%
	<i>Corylus heterophylla</i>	2% (L)	0%	1% (L)	1% (L)
		0%	0%	0%	4% (L, S)
<i>Celastraceae</i>	<i>Celastrus orbiculatus</i>	2% (F)	0%	0%	1% (F)
		0%	0%	3% (F)	4% (F)

Family	Food Species	NLF	LF	AM	J
<i>Cornaceae</i>	<i>Cornus sp</i>	10% (F)	20% (F)	27% (F)	30% (F)
		0%	0%	0%	0%
	<i>Swida macrophylla</i>	0%	0%	0%	0%
		0%	0%	6% (L)	0%
<i>Fagaceae</i>	<i>Quercus aliena</i>	2% (L)	0%	0%	0%
		7% (S)	8% (S)	18% (S)	13% (S)
<i>Hydrangeaceae</i>	<i>Deutzia vilmorinae</i>	0%	1% (L)	0%	0%
		7% (L)	0%	0%	4% (L)
<i>Lamiaceae</i>	<i>Glechoma longituba</i>	0%	0%	0%	0%
		0%	0%	6% (L)	0%
<i>Lauraceae</i>	<i>Lindera obtusiloba</i>	19% (F)	21% (F)	23% (F)	19% (F, L)
		0%	0%	0%	0%
	<i>Litsea rubescens</i>	13% (F)	8% (F)	11% (F)	9% (F)
		0%	0%	0%	2% (L)
<i>Moraceae</i>	<i>Morus alba</i>	26% (L)	21% (L)	28% (L)	21% (L)
		25% (L)	19% (L)	24% (L)	21% (L)
<i>Oleaceae</i>	<i>Fraxinus mandshurica</i>	0%	0%	0%	0%
		0%	8% (B)	3% (B)	0%

Family	Food Species	NLF	LF	AM	J
<i>Pinaceae</i>	<i>Pinus massoniana</i>	0%	0%	0%	0%
		29% (S)	19% (S)	24% (S)	13% (S)
<i>Rosaceae</i>	<i>Padus asiatica</i>	3% (L)	4% (L)	6% (F, L)	1% (L)
		0%	12% (B, L)	0%	4% (L)
	<i>Prunus salicina</i>	6% (L)	4% (L)	0%	3% (L)
		4% (L)	0%	0%	0%
	<i>Prunus armeniaca</i>	0%	1% (L)	1% (L)	0%
		0%	8% (L)	3% (L)	0%
	<i>Malus baccata</i>	0%	0%	0%	0%
		4% (F)	4% (F)	0%	0%
	<i>Padus sp</i>	0%	0%	0%	0%
		4% (L)	0%	3% (L)	0%
<i>Rosaceae</i>	<i>Prunus pleiocerasus</i>	2% (L)	0%	0%	1% (L)
		0%	0%	0%	0%
	<i>Crataegus cuneata</i>	0%	0%	0%	2% (F)
		0%	0%	0%	0%
<i>Sabiaceae</i>	<i>Meliosma cuneifolia</i>	0%	1% (L)	0%	1% (L)

Family	Food Species	NLF	LF	AM	J
<i>Sabiaceae</i>	<i>Meliosma cuneifolia</i>	0%	0%	0%	0%
<i>Salicaceae</i>	<i>Salix matsudana</i>	2% (L)	0%	0%	1% (L)
		4% (L)	0%	0%	0%
	<i>Salix sp</i>	0%	0%	0%	0%
		0%	0%	0%	2% (L)
<i>Schisandraceae</i>	<i>Schisandra chinensis</i>	0%	0%	0%	0%
		0%	0%	3% (L)	2% (L)
<i>Stachyuraceae</i>	<i>Stachyurus chinensis</i>	0%	0%	0%	2% (L)
		0%	0%	0%	0%
<i>Tiliaceae</i>	<i>Grewia biloba</i>	8% (L)	13% (L)	1% (L)	7% (L)
		4% (L)	12% (B, L)	3% (L)	11% (L)
<i>Ulmaceae</i>	<i>Ulmus bergmanniana</i>	0%	0%	0%	0%
		4% (L)	0%	0%	4% (L)
	<i>Ulmus macrocarpa</i>	0%	0%	1% (L)	0%
		0%	0%	0%	4% (L)
Unknown	Ma Huan Shao	0%	0%	0%	0%
		0%	4% (S)	0%	4% (L)

Family	Food Species	NLF	LF	AM	J
	Qing Lian Zhi	3% (L)	0%	0%	1% (L)
		0%	0%	0%	2% (L)
	Unidentified Fungus	0%	0%	0%	0%
		4% (FB)	0%	0%	0%
	Qing Gang Mu	0%	0%	0%	0%
		4% (L)	0%	0%	0%
	Huang Bo	0%	0%	0%	0%
		0%	0%	3% (F)	0%
	Ji liu	0%	1% (L)	0%	0%
		0%	0%	0%	0%
	Ku Dong Po	0%	0%	0%	0%
		0%	0%	0%	2% (L)

Table A1.3. The proportional nutritional composition of foods consumed by the provisioned troop during summer and autumn. Foods are sorted by their contribution to the troop's diet (by weight). UI=foods not indentifiable.

Food Item	Part	% CP	% Lipids	% NSC	% NDF	% Lignin	% Diet	Season
Apple	Whole	0.024	0.117	0.700	0.115	0.044	55%	Autumn
Apple	Whole	0.024	0.117	0.700	0.115	0.044	44%	Summer
Carrot	Whole	0.144	0.059	0.500	0.245	0.052	23%	Autumn
Dried Corn	Seeds	0.107	0.051	0.659	0.160	0.023	21%	Summer
Dried Corn	Seeds	0.107	0.051	0.659	0.160	0.023	15%	Autumn
Peach	Pulp	0.106	0.111	0.579	0.141	0.063	13%	Summer
Carrot	Whole	0.144	0.059	0.500	0.245	0.052	8%	Summer
Banana	Pulp	0.078	0.267	0.512	0.082	0.062	6%	Summer
Banana	Skin	0.088	0.091	0.243	0.472	0.105	4%	Summer
Banana	Pulp	0.078	0.267	0.512	0.082	0.062	3%	Autumn
UI-1	Bark	0.061	0.069	0.148	0.547	0.175	2%	Autumn
Parsnip	Whole	0.163	0.058	0.430	0.259	0.090	1%	Summer
Banana	Skin	0.088	0.091	0.243	0.472	0.105	1%	Autumn
Peanuts	Seeds	0.242	0.467	0.080	0.129	0.082	1%	Summer
<i>Toxicodendron vernicifluum</i>	Leaves	0.218	0.046	0.118	0.435	0.183	1%	Summer
UI-1	Leaves	0.297	0.053	0.198	0.397	0.056	0%	Summer
<i>Juglans cathayensis</i>	Leaves	0.209	0.071	0.183	0.455	0.082	0%	Summer
<i>Acer sp</i>	Leaves	0.173	0.090	0.031	0.570	0.137	0%	Autumn
<i>Quercus aliena</i>	Leaves	0.186	0.031	0.200	0.503	0.079	0%	Summer
UI-2	Bark	0.057	0.029	0.126	0.578	0.209	0%	Autumn

Food Item	Part	% CP	% Lipids	% NSC	% NDF	% Lignin	% Diet	Season
<i>Quercus sp</i>	Leaves	0.154	0.087	0.113	0.484	0.162	0%	Autumn
<i>Actinidia kolomikta</i>	Bark	0.091	0.026	0.191	0.618	0.074	0%	Summer
<i>Quercus aliena</i>	Leaves	0.162	0.101	0.153	0.467	0.116	0%	Autumn
UI-2	Stems	0.132	0.025	0.144	0.566	0.133	0%	Summer
Peach	Pit	0.001	0.529	0.123	0.257	0.089	0%	Summer
<i>Quercus aliena</i>	Bark	0.056	0.027	0.187	0.579	0.150	0%	Autumn
<i>Vitis piasezkii</i>	Leaves	0.233	0.103	0.217	0.343	0.105	0%	Summer
<i>Aralia elata</i>	Bark	0.060	0.022	0.062	0.623	0.233	0%	Summer
<i>Fraxinus mandshurica</i>	Bark	0.060	0.026	0.130	0.549	0.235	0%	Summer
<i>Litsea rubescens</i>	Leaves	0.197	0.058	0.274	0.393	0.078	0%	Summer
<i>Grewia biloba</i>	Bark	0.068	0.015	0.078	0.575	0.265	0%	Summer

Table A1.4. The nutrient content of foods consumed by the spider monkey troop (AP=available protein, NSC=non-structural carbohydrates, ADF=acid detergent fibre, l=leaf, s=stalk, a=apricot, p=plain, *=undetermined). All nutrient values are presented as percentage of dry matter. Underlined values were determined in our lab. All other data were collected from the following: Zootrition, published data (Al-Sayed & Ahmed 2013; Belitz et al. 2009; Fuller 2004; Ghaly & Alkoaik 2009; Schmidt et al. 2005; van Huis et al. 2013)(Al-Sayed & Ahmed 2013; Belitz et al. 2009; Fuller 2004; Ghaly & Alkoaik 2009; Schmidt et al. 2005; van Huis et al. 2013)(Al-Sayed & Ahmed 2013; Belitz et al. 2009; Fuller 2004; Ghaly & Alkoaik 2009; Schmidt et al. 2005; van Huis et al. 2013), product suppliers, product nutrient labels, national nutrient databases (USA, Canada, Australia, New Zealand, and the UK).

Food Item	% AP	% Lipids	% NSC	% ADF	% Ash
apple	<u>1.090%</u>	2.889%	86.163%	<u>7.769%</u>	2.089%
apricot preserve	0.927%	0.000%	<u>96.559%</u>	2.513%	*
banana pulp	<u>5.315%</u>	2.753%	78.761%	<u>8.567%</u>	4.603%
banana skin	<u>5.357%</u>	<u>10.785%</u>	<u>23.908%</u>	<u>37.604%</u>	22.346%
beetroot	<u>14.324%</u>	1.547%	65.109%	<u>9.196%</u>	9.824%
bok choy (l)	<u>18.296%</u>	3.958%	<u>23.947%</u>	<u>37.968%</u>	15.832%
bok choy (s)	<u>26.258%</u>	<u>6.809%</u>	<u>13.612%</u>	<u>27.735%</u>	<u>25.586%</u>
broccoli florettes	<u>37.783%</u>	4.556%	26.310%	<u>19.378%</u>	11.973%
broccoli (s)	<u>48.680%</u>	5.736%	<u>1.478%</u>	<u>29.031%</u>	15.074%
cabbage	<u>18.900%</u>	3.664%	47.999%	<u>19.808%</u>	9.629%
capsicum (green)	<u>13.181%</u>	3.090%	54.966%	<u>23.880%</u>	4.883%
capsicum (red)	<u>12.500%</u>	2.660%	67.543%	<u>13.095%</u>	4.203%
capsicum (yellow)	<u>26.767%</u>	6.680%	<u>7.770%</u>	<u>44.459%</u>	14.324%
carrot	<u>14.138%</u>	2.750%	51.816%	<u>18.727%</u>	12.569%
celery (l)	<u>32.855%</u>	15.036%	<u>1.525%</u>	<u>28.095%</u>	<u>22.489%</u>
celery (s)	<u>15.616%</u>	3.924%	42.239%	<u>20.911%</u>	17.311%
coconut	<u>4.164%</u>	41.889%	5.567%	<u>46.548%</u>	1.833%
corn	<u>23.759%</u>	9.570%	51.370%	<u>10.273%</u>	5.029%
cucumber (skinless)	<u>19.725%</u>	5.463%	53.493%	<u>11.759%</u>	9.561%
cucumber (whole)	<u>20.356%</u>	4.318%	35.327%	<u>24.784%</u>	15.216%

Food Item	% AP	% Lipids	% NSC	% ADF	% Ash
date	<u>2.442%</u>	0.636%	87.639%	<u>7.048%</u>	2.236%
egg (whole)	52.340%	40.426%	2.979%	0.000%	4.255%
egg (white)	92.199%	0.000%	2.837%	0.000%	4.965%
egg (yolk)	33.333%	63.273%	0.399%	0.000%	2.994%
grapefruit	<u>7.370%</u>	1.304%	72.853%	<u>14.443%</u>	4.030%
grapes	<u>5.494%</u>	1.333%	84.644%	<u>3.863%</u>	4.665%
green beans	<u>20.342%</u>	1.379%	52.825%	<u>17.851%</u>	7.603%
honeydew	<u>3.969%</u>	0.982%	80.751%	<u>8.426%</u>	5.872%
kibble	<u>34.145%</u>	21.900%	<u>18.589%</u>	<u>19.261%</u>	<u>6.106%</u>
kiwi pulp	<u>6.563%</u>	3.307%	67.542%	<u>17.779%</u>	4.808%
kiwi skin	<u>6.706%</u>	<u>9.394%</u>	<u>30.547%</u>	<u>40.461%</u>	<u>12.892%</u>
kumara	<u>7.916%</u>	0.091%	80.136%	<u>7.854%</u>	4.004%
lentil ball	<u>45.101%</u>	1.614%	39.484%	<u>9.258%</u>	4.543%
lettuce	<u>23.011%</u>	2.335%	46.002%	<u>19.312%</u>	9.340%
mealworm	51.684%	37.053%	0.000%	6.000%	5.263%
onion	<u>17.195%</u>	2.469%	64.416%	<u>10.203%</u>	5.717%
orange pulp	<u>7.646%</u>	0.984%	78.699%	<u>7.753%</u>	4.919%
orange skin	<u>16.637%</u>	<u>2.755%</u>	<u>22.035%</u>	<u>51.041%</u>	7.533%
parsley (l)	<u>33.841%</u>	1.960%	4.900%	<u>36.756%</u>	22.542%
parsley (s)	<u>17.947%</u>	<u>10.021%</u>	<u>5.889%</u>	<u>34.250%</u>	<u>31.892%</u>
parsnip	<u>6.995%</u>	1.933%	69.033%	<u>15.740%</u>	6.298%
pawpaw	<u>4.020%</u>	1.332%	77.165%	<u>11.662%</u>	5.820%
Peanut Butter	29.669%	51.715%	8.726%	6.799%	3.091%
peanuts	<u>25.046%</u>	32.367%	7.909%	<u>32.737%</u>	1.940%
pear	<u>2.184%</u>	2.906%	75.950%	<u>16.925%</u>	2.035%
peas (frozen)	<u>45.565%</u>	3.272%	19.612%	<u>24.633%</u>	6.918%
Peas/corn mix	<u>9.211%</u>	3.227%	78.065%	<u>5.983%</u>	3.514%
pineapple	<u>3.358%</u>	4.221%	83.961%	<u>5.615%</u>	2.845%
popcorn	<u>13.240%</u>	5.280%	70.933%	<u>8.280%</u>	2.266%
potato	<u>12.117%</u>	0.594%	77.872%	<u>4.182%</u>	5.235%
pumpkin	<u>16.731%</u>	1.796%	<u>46.060%</u>	<u>21.040%</u>	14.372%
pumpkin skin	<u>15.500%</u>	<u>7.063%</u>	17.289%	<u>45.791%</u>	<u>14.356%</u>
pumpkin seeds	<u>26.265%</u>	48.959%	14.728%	<u>4.788%</u>	5.261%
raisin	<u>3.656%</u>	0.600%	89.148%	<u>4.275%</u>	2.321%
rockmelon	<u>9.085%</u>	2.891%	73.624%	<u>7.067%</u>	7.333%
Seed mix	<u>23.526%</u>	24.654%	<u>40.481%</u>	<u>7.304%</u>	<u>4.034%</u>
silver beet (l)	<u>20.621%</u>	3.078%	<u>18.451%</u>	<u>33.223%</u>	24.627%
silver beet (s)	<u>20.441%</u>	<u>7.820%</u>	<u>11.000%</u>	<u>26.772%</u>	<u>33.966%</u>
Soup/ mix	<u>1.663%</u>	2.288%	<u>52.150%</u>	<u>4.959%</u>	<u>38.940%</u>
spinach (l)	<u>34.859%</u>	4.680%	9.890%	<u>24.397%</u>	<u>26.174%</u>
spinach (s)	<u>24.107%</u>	<u>7.392%</u>	<u>12.297%</u>	<u>17.986%</u>	<u>38.218%</u>
spring onion (l)	<u>20.826%</u>	<u>13.128%</u>	<u>17.476%</u>	<u>31.610%</u>	<u>16.960%</u>
spring onion (s)	<u>23.292%</u>	<u>2.118%</u>	<u>29.790%</u>	<u>32.390%</u>	<u>12.409%</u>

Food Item	% AP	% Lipids	% NSC	% ADF	% Ash
strawberry jam	1.437%	0.000%	<u>98.563%</u>	0.000%	*
swede	<u>11.473%</u>	1.336%	63.120%	<u>14.717%</u>	9.354%
tangelo pulp	<u>9.003%</u>	1.011%	78.821%	<u>7.123%</u>	4.042%
tangelo skin	<u>12.222%</u>	<u>8.277%</u>	<u>29.328%</u>	<u>39.834%</u>	<u>10.339%</u>
tomato	<u>13.747%</u>	5.494%	57.137%	<u>16.633%</u>	6.989%
watermelon	<u>7.122%</u>	5.367%	79.868%	<u>4.398%</u>	3.246%
watermelon rind	0.548%	4.792%	70.753%	*	23.907%
yogurt (a)	<u>13.346%</u>	12.183%	55.583%	<u>5.560%</u>	<u>13.327%</u>
yogurt (p)	<u>19.522%</u>	2.371%	36.225%	<u>8.369%</u>	<u>33.513%</u>