University of Calgary

PRISM Repository **https://prism.ucalgary.ca**

The Vault Open Theses and Dissertations

2013-08-27

The Use of Fallback Foods in a Population of Black Handed Spider Monkeys at Runaway Creek Nature Reserve, Belize

Griffin, Neil

Griffin, N. (2013). The Use of Fallback Foods in a Population of Black Handed Spider Monkeys at Runaway Creek Nature Reserve, Belize (Master's thesis, University of Calgary, Calgary, Canada). Retrieved from https://prism.ucalgary.ca. doi:10.11575/PRISM/28409
http://hdl.handle.net/11023/896
Downloaded from PRISM Repository, University of Calgary

UNIVERSITY OF CALGARY

The Use of Fallback Foods in a Population of Black Handed Spider Monkeys at Runaway Creek Nature Reserve, Belize

by

Neil Christopher Griffin

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

CALGARY, ALBERTA

AUGUST, 2013

© Neil Christopher Griffin 2013

Abstract

Seasonal fluctuations in preferred food availability cause some non-human primate species to occasionally rely on less-preferred food types, called fallback foods. Periodic reliance on fallback foods has led, in some cases, to the evolution of morphological traits geared towards their exploitation. However, in species without these traits, fallback foods may instead beget behavioural modifications. Using 21 months of data, I analysed the use of fallback foods, and their behavioural consequences, in a population of highly frugivorous spider monkeys. Spider monkeys have previously been suggested to fall back on leaves, however I found that flowers, not leaves, were used as a fallback food. Seasonal reliance on flowers led to decreases in time spent travelling and increases in time spent feeding, as well as decreases in subgroup size. I interpreted these behaviours as an energy-minimizing strategy adopted to offset the low per-capita energy available in flowers as compared to fruit.

Acknowledgments

In using pre-collected data, I owe a tremendous debt to the field researchers who came before me, and slogged and toiled for months, habituating and chasing the monkeys of Runaway Creek through their tortuous environment: Gilroy Welch, Stevan Renault, Brittany Dean, Kayley Evans, Kayla Hartwell, Jane Champion, and untold numbers of research assistants. Without their time and dedication, this research would have been impossible. The spider monkey research group at the University of Calgary was invaluable in providing feedback, criticism, commentary, and support; thank you, Dr Mary Pavelka, Dr Hugh Notman, Tracy Wyman, Jane Champion, Colin Dubreuil, and Meredith Brown. I'd also like to thank Dr John Carroll and Dr Peter Griffin for their helpful comments and criticisms on earlier drafts of this manuscript. Additional thanks to Birds Without Borders, the Forestry Department of Belize, and the Government of Belize, as well as my committee members, Dr Linda Fedigan and Dr Warren Wilson.

Dedication

To my parents, Debbie and Peter, for never asking me to get a real job.

And Laura, for her encouragement and support.

Table of Contents

Abstract ii

Acknowledgments iii

Dedication iv

Table of Contents v

List of Tables vi

List of Figures and Illustrations vii

Chapter One: Literature Review 1
- Fallback foods: of finches and fish 1
- Fallback foods in nonhuman primates 3
- Morphological responses to fallback foods 5
- Behavioural responses to fallback foods 7
- Nutritional ecology 8
- The diets of spider monkeys 10
- Study objectives 13

Chapter Two: Methods 14
- Study Site 14
- Study Subjects 16
- Data Collection 16
  - *Vegetation and environmental data* 16
  - *Behavioural data* 17
- Data Analyses 18
  - *Calculation of plant part availability* 18
  - *Modelling plant part selection* 19
  - *Modelling the effect of fallback food consumption on activity budgets* 20
  - *Modelling the effect of fallback food on subgroup size* 21

Chapter Three: Results 22
- Diet overview 22
- Plant part availability 28
- Plant part selection: flowers as a fallback food 30
- The effect of fallback food consumption on monthly activity budgets 33
- The effect of fallback food consumption on subgroup size 38

Chapter Four: Discussion 40
- Folivory in spider monkeys at Runaway Creek 40
  - *Why are females more likely to eat leaves?* 41
- Falling back on flowers 42
- The effects of flower eating on activity budgets and subgroup size 44
- Where do flowers fit in the fallback food frameworks? 46
- Directions for Future Research 47

Literature Cited 49

Appendix A 57

Appendix B 58

Appendix C 62

List of Tables

Table 1. Composition of a black handed spider monkey group at Runaway Creek, Belize during 2009 and 2010. 16
Table 2. Small-Hsiao test of the assumption of IIA. The test meets assumptions (all p values are >0.05). 20
Table 3. Tree species that accounted for at least 1% of total ripe fruit consumption during the study period, and the proportion of total frugivory for which they were responsible. 24
Table 4. Tree species that accounted for at least 1% of total leaf consumption during the study period, and the proportion of total folivory for which they were responsible. 25
Table 5. Tree species from which spider monkeys ate flowers during the study period, and the proportion of total flower-eating for which each species was responsible. 26
Table 6. Average monthly availability and monthly percent of trees in a phenological phase between January 2009 and October 2010. Based on monthly surveys of 172 trees, presented as means +/- 1 SE. 28
Table 7. Plant part selection model coefficients calculated based on 1453 scan samples collected between January 2009 and October 2010. Coefficients reported here are based on a model bootstrapped 1000 times. Bolded times are significant (p<0.05). The independent variables were sex, age, individual ID and ripe fruit availability (RFA). The dependent variable was plant part (flowers, leaves, or ripe fruit). Ripe fruit was the reference category, and therefore is not presented here. 31
Table 8. Main effect results for a GLM with flower consumption, sex, and age as independent variables and the proportion of scans spent feeding, socializing, and travelling as the dependent variables. Based on data collected between January 2009 and October 2010. N = 69 age-sex class/month categories. Interactions were largely non-significant, and so are excluded here. The complete model table can be found in Appendix C. 35

List of Figures and Illustrations

Figure 1. Monthly average precipitation, and minimum and maximum temperatures at Runaway Creek, Belize. Data taken from the Philip S.W. Goldson International Airport weather station, located approximately 50km from the field site..... 15
Figure 2. Average monthly flower consumption during 2009 and 2010. Data were not collected in December. The period from January to April accounts for 92.1% of all observed flower consumption during the study period..... 27
Figure 3. Food availability scores at Runaway Creek between January 2009 and October 2010. Based on monthly phenology scores, calculated from a phenology trail of 172 trees from 34 species..... 29
Figure 4. Predicted probabilities of plant part consumption for male and female black-handed spider monkeys at Runaway Creek across a range of ripe fruit availability scores. Females were significantly more likely than males to consume leaves (b, $p < 0.05$). The negative relationship between flower consumption and ripe fruit availability was also significant (c, $p < 0.001$). Based on 1453 scans collected between January 2009 and October 2010..... 32
Figure 5. The relationship between flower consumption and ripe fruit availability over 21 months at Runaway Creek, Belize. The relationship is significant: as ripe fruit availability increased, flower consumption decreased significantly ($\beta = -151$, CI: -186 to -120, $p = 0.001$).....33
Figure 6. The relationship between feeding and monthly flower consumption for the spider monkeys at Runaway Creek. The relationship is significant (F = 3.269, df = 13,20, p = 0.009). As flower consumption increased, so did the proportion of time spent feeding.. 36
Figure 7. The relationship between travelling and monthly flower consumption. The relationship is significant (F = 5.381, df = 13,20, p = 0.000). As flower consumption increased, the proportion of time spent travelling decreased..... 37
Figure 8. Frequency of subgroup sizes observed at Runaway Creek, based on 1599 scan samples of subgroups. The most frequent subgroup size was two individuals, and the mean was 4.44 individuals..... 38
Figure 9. The relationship between average monthly subgroup size and the proportion of flowers in the diet. The relationship was significant (generalized linear model: z = -12.25, p = 0.000). As the proportion of flowers in the diet increased, the average subgroup size decreased..... 39

Chapter One: Literature Review

Fallback foods: of finches and fish

In the 1980s, icthyologist Karel Liem made an observation: some aquatic species of animal had highly specialized feeding morphologies, but ate generalized diets (Liem, 1990). This apparent incongruity between form and function, called Liem's Paradox, was originally attributed to genetic constraints on evolution, and caused some ecologists to rethink the role that dietary niches played in speciation (Liem, 1990; Constantino and Wright, 2009). However, ten years later, a different explanation for the paradox was proposed.

Instead of a genetic constraint, the presence of specialized morphology may be a specific adaptation for survival in times of food scarcity (Robinson and Wilson, 1998). Specialized morphology would allow a species to occupy a narrow niche in times of food scarcity, reducing competition with conspecifics, while taking advantage of a generalized diet in times of abundance. As long as the specialized morphology did not impede generalist feeding, then the species would be able to forage optimally regardless of food availability (Robinson and Wilson, 1998). In times of scarcity, a species falls back on the specialized food that it can monopolize, and in times of abundance, it consumes widely available food. This answer to Liem's Paradox has since found support when applied retroactively to studies of Darwin's finches on the Galapagos Islands, and freshwater cichlid fish.

The finches of the Galapagos Islands hold a special place in biology as an example of adaptive radiation, but they have also been used to illustrate the concept of fallback foods and their role in a species evolution. Darwin's finches comprise a group of 4 genera and 14 species, 13 of which

are endemic to the Galapagos. Of these, the most well-known are the ground finches (genus *Geospiza*) - a genus of six species studied for the niche differentiation caused by variation in their beak sizes and diets. During the wet season, sympatric species ate a common diet of fruit and seeds. But during the dry season, when fruit and seeds were scarce, the species' diets diverged, with each species eating foods that reflected their specialized beak morphology (Smith et al., 1978).

The second inspiration for fallback food theory was the cichlids (Cichlidae), a widespread genus of freshwater fish best known for their diversity of species, particularly in the East African Great Lakes (Takahashi and Koblmüller, 2011). The three major lakes of the East African Rift Valley (Lake Victoria, Lake Malawi, and Lake Tanganyika) are together home to more than 800 species of cichlid (Takahashi and Koblmüller, 2011). Within the lakes, the species occupy highly specialized dietary niches: some are dedicated scale eaters, others are piscivorous, and still others suck algae from substrate. These dietary niches are reflected by specialized feeding morphology (Liem, 1973). However, when presented with easily digestible, free-floating food, all of the specialized species are capable of eating a general diet. When such food is rare, the species fallback on the foods requiring their specialized morphology (Meyer, 1989). Cichlid feeding morphology, like the beak shape of Darwin's finches, reflects their feeding strategies in times of rarity, rather than in times of abundance - emphasizing the important role that fallback foods may play in a species evolution (Constantino and Wright, 2009). Since Robinson and Wilson's 1998 explication, the study of fallback foods has mostly taken place within the context of understanding the evolution and ecology of nonhuman primates (Constantino and Wright, 2009).

Fallback foods in nonhuman primates

The diets of nonhuman primates are diverse, and while species are generally considered to be "frugivores", "folivores" or "insectivores" based on their primary food choice, secondary food types may be equally important in understanding a species ecology (Lambert, 2011). Assessing the relative importance of a food in a species diet depends on a number of factors. These include how often the food is available, how often it is eaten, how much of the diet it comprises, and how often it is eaten in relation to the availability of both itself and of other foods (Leighton, 1993; Lambert, 2011). Using these factors, foods can be broadly placed into three categories: staple foods, preferred foods, and fallback foods (Marshall and Wrangham, 2007). Preferred foods are over-selected, meaning they are eaten more frequently than predicted by chance, based on their environmental availability (Leighton, 1993). Preferred foods are characterized by high energy content or ease of handling, and when available account for a large proportion of a primates diet (Marshall and Wrangham, 2007). Staple food items are consistent in a diet throughout the year, and their consumption does not correlate strongly with the availability of other food sources (Doran et al., 2002). These foods may be readily abundant, or comparatively rare in the environment, and are often perceived as lower quality than preferred foods. However, their consumption may be tied to nutrient balancing - staple foods may be an important source of nutrients unavailable in other foods (Knott, 2005). Fallback foods, the third category, are traditionally defined as a food type whose presence in the diet correlates negatively with the availability of a preferred food (Marshall and Wrangham, 2007).

Recently researchers have developed two separate-but-complementary frameworks for understanding fallback foods in greater detail (Marshall et al., 2009). The first framework,

developed by Lambert (2007), divides fallback foods into two categories based on the nutritional density of the food item. Different species rely on fallback foods that either have a high nutritional density or a low nutritional density, and these nutritional characteristics determine how a species may be adapted to utilize the food. Low nutrition fallback foods, like leaves, may lead to morphological adaptations for their efficient exploitation. These foods tend to be widely dispersed and easy to find, but difficult in terms of nutrient extraction. High nutrition fallback foods, like palm nuts and termite mounds, are difficult to find or access, and have a nutritional content that is not appreciably different from preferred foods. The use of high nutrition fallback foods leads to behavioural adaptations, including changes in activity budgets or the development of tool-use (Lambert 2007).

The second framework, developed by Marshall and Wrangham (2007) divides fallback foods into two categories based on their consumption: staple fallback foods and filler fallback foods. Staple fallback foods are those which are always present in a primate's diet, and occasionally account for 100% of the diet (for example, leaves for proboscis monkeys, *Nasalis larvatus* (Yeager, 1989)); filler fallback foods never make up 100% of the diet, and are absent completely when preferred foods are widely abundant (for example, cambium in the diet of Bornean orangutans, *Pongo pygmaeus* (Leighton, 1993)). Staple fallback foods, because they occasionally account for 100% of a primate's diet, may play a critical role in primate evolution. During periods of time when preferred foods are unavailable and a species is relying completely on a staple fallback food, individuals who have traits adapted for the use of those foods will be better able to survive than individuals lacking such adaptations (Marshall et al., 2009). This differential

survival in times of food scarcity results in strong selection for behavioural or morphological adaptions for the utilization of fallback foods.

Together these frameworks lead to a theoretical basis for understanding the use of fallback foods (Marshall et al., 2009). High nutrient density fallback strategies are likely to use filler fallback foods; low nutrient density fallback strategies are more likely to use staple fallback foods (Lambert 2007, Marshall and Wrangham, 2007; Marshall et al., 2009). Low quality fallback foods are likely to drive morphological adaptations because they are easy to find, but difficult to handle, while high quality fallback foods, which are more difficult to find, but easy to handle, will drive behavioural adaptations (Marshall et al., 2009). While neither framework is applicable in all situations (few primate species eat a monotypic diet for long periods of time, the requirement for a staple fallback food), together they are useful for providing a model on which to base investigation of fallback foods in a nonhuman primates diet (Krishnadas et al., 2011).

Morphological responses to fallback foods

Both frameworks hypothesize that the use of fallback foods can lead to morphological adaptations required for efficient exploitation. In nonhuman primates, research has been particularly focused on adaptations in dental and digestive anatomy. Preferred food items (e.g. ripe fruit) are easily handled by most dental formations but fallback foods may require specializations for processing exceptionally hard or tough materials, such as seeds or leaves (Marshall and Wrangham, 2007). Similarly, fallback foods, especially leaves, are assumed to be more difficult to digest than preferred foods, requiring specific adaptations in the digestive system including forestomach fermentation or longer guts (Marshall and Wrangham, 2007).

Because fallback foods are more difficult to process than preferred foods, and important in times when high food scarcity is causing increased mortality, species which rely on staple fallback foods should display a morphology adapted for fallback, rather than preferred, foods (Robinson and Wilson, 1998; Marshall and Wrangham, 2007).

In a study of sympatric guenon (*Cercopithecus ascanius*) and mangabey (*Lophocebus albigena*) species, Lambert et al. (2004) found that the dietary niches of the two species overlapped in times of ripe fruit abundance, but diverged when ripe fruit was not available, with the mangabey exploiting a difficult-to-process diet of bark and seeds during periods of scarcity. They found that mangabeys had thicker dental enamel which allowed them access to hard foods, and argued that the evolution of this enamel was driven by the use of bark and seeds as fallback foods (Lambert et al., 2004).

Other studies have found similar evidence in titi monkeys (*Callicebus sp.*)(Kinzey 1978), lemurs (Yamashita, 1998), and African great apes (Ungar, 2004): some species which undergo periodic food scarcity have evolved morphological adaptations which are specialized for their fallback, rather than their preferred, foods. However, many primate species experience food scarcity, while only a few display obvious morphological adaptations for using fallback foods. In these other species the ability to adequately exploit fallback foods may come from behavioural, rather than morphological, changes (Lambert, 2007; Altmann, 2009).

Behavioural responses to fallback foods

Comparatively little attention has been paid to the short-term behavioural consequences of using fallback foods (Knott, 2005), though their occurrence is well-established (Oates, 1987). Altmann (2009) summarizes the varied behavioural responses a species may exhibit in response to periods of food scarcity, including minimizing energy expenditure by travelling less and resting more, and accounting for the poorer nutritional quality associated with fallback foods by increasing the amount of time spent feeding. For example, when relying on fallback foods in periods of food scarcity, both Bornean orangutans (*Pongo pygmaeus*) (Knott, 1999) and Western lowland gorillas (*Gorilla gorilla gorilla*) (Goldsmith, 1999) decreased their average day ranges and the amount of time spent travelling. This response is not uniform however, and both yellow baboons (Altmann 2009) and lion-tailed macaques (*Macaca silenus*) (Krishnadas et al., 2011) have been observed to increase the time spent travelling while relying on fallback foods. In the case of baboons, this increased travel time was associated with an increase in the amount of time spent foraging and feeding, a result also seen in chimpanzees (*Pan troglodytes*) (Doran, 1997), which spent more time feeding in months of low fruit availability than in months of high fruit availability. Wallace (2005) found that in periods of low fruit availability, black spider monkeys (*Ateles chamek*) spent more time resting and less time moving, but did not change the amount of time spent feeding. Behavioural responses to the use of fallback foods in times of resource scarcity are varied, both by species and environment, but they are pronounced, and a larger body of research would help to increase understanding of them (Knott, 2005).

In addition to activity budget changes, the use of fallback foods may lead to changes in within-group social organization (Altmann, 2009). Nonhuman primate group size, and the levels of within-group aggression, are often assumed to result from the availability of contestable food resources (Wrangham, 1979; 1980). When a food resource can be monopolized, has a high nutritional content, and is presumed to occur in defendable patches (i.e. fruit), primates are expected to have higher rates of within-group aggression and to forage in smaller groups to avoid contest competition (Schoener, 1971; Norconk and Kinzey, 1994). If a food resource is widely abundant and cannot be monopolized, as leaves are generally characterized, the reduction in competition may allow frugivorous primates to live in larger subgroups. This pattern may not be true for folivorous monkeys, which live in small groups despite relying on an abundant food source (Steenbeek and van Schaik, 2001; Chapman and Pavelka, 2004), but nonetheless, in primarily frugivorous primates subgroup size appears to be positively correlated with the availability of food in the environment (Doran, 1997; Grueter et al., 2009; Riedel et al., 2010; Chancellor et al., 2011).

Nutritional ecology

Nutritional ecology is the study of how primates meet their nutritional needs (Lambert, 2011). Many nonhuman primates are eclectic omnivores, eating from some combination of fruit, leaves, flowers, insects, soil, sap, bark, seeds, lizards, and eggs. This dietary diversity may be necessary for primates to acquire the micro- and macro- nutrients necessary for survival, including carbohydrates, lipids, proteins and mineral ions (Lambert, 2011). In low trophic level foods (particularly plant parts), the composition and availability of these nutrients varies widely, with fruits tending to be higher in accessible energy, but low in protein, and leaves having higher

levels of protein, but lower amounts of accessible energy (Milton, 1979; 1984; Ruby, 2000; Behie and Pavelka, 2012a). As all of these nutrients are necessary for a complete diet (Lambert, 2011), this variability in nutrient availability suggests that for a diet to be nutritionally complete it may need to be biologically diverse. Primate researchers have highlighted five models of how primates attempt to reach nutritional goals: 1) energy maximization, 2) nitrogen maximization, 3) avoidance of plant secondary metabolites, 4) limiting dietary fibre, and 5) nutrient balancing (Felton et al., 2009a). The fifth model, nutrient balancing, may be of particular importance to frugivorous primates (Vogel et al., 2011).

The study of nutrient balancing in frugivorous primates is focused on how they acquire protein. Protein is an essential macronutrient for growth and development, DNA replication, and cellular function, but is a limiting resource for animals in many terrestrial ecosystems, owing both to the relative scarcity of biologically usable protein present in the environment, and the relative inefficiency with which most animals assimilate and recycle it (Mattson, 1980; White, 1993; Rothman et al., 2008a). For an herbivorous tropical mammal, leaves are the most accessible source of protein (as well as the best source of many minerals) (Milton, 1984; Ruby, 2000; Milton, 2006; Behie and Pavelka, 2012b; a). Fruit, on the other hand, is a relatively poor source of protein, though a good source of carbohydrates and sugars (Milton, 1984; Ruby, 2000; Lambert, 2011; Vogel et al., 2011). The low availability of protein in tropical fruits may leave tropical mammals which rely primarily on fruit for their diet at risk for protein deficiency (Courts, 1998; Ruby, 2000; Herrera et al., 2002; Felton et al., 2009a; b; 2009c), which has consequences including lower weight, decreased growth rate, increased infant mortality, and subsequently lower fitness (Riopelle et al., 1974; Fleagle et al., 1975; Riopelle et al., 1975).

Tropical frugivores may acquire the necessary levels of protein by balancing their intake of high energy fruits with more proteinaceous foods (Courts, 1998; Herrera et al., 2002; Felton et al., 2009b; c). In frugivorous bats, a group of animals in which nutrient balancing has been well-studied, some species of Old World fruit bat (the Pteropodidae) supplement their protein-poor frugivorous diet with bouts of insectivory, folivory (Ruby, 2000), or by feeding on carrion (reviewed in Courts 1998 and Herrera et al. 2002). Non-human primates have also been suggested to selectively feed on protein-rich foods (Conklin-Brittain et al., 1998; Ganas et al., 2008; Rothman et al., 2008b; Felton et al., 2009c), and to modify their feeding habits to maintain constant levels of protein intake (Yamashita, 2008; Felton et al., 2009b).

The diets of spider monkeys

Spider monkeys (the genus *Ateles*) are generally considered ripe fruit specialists, and the annual diet of most studied populations ranges between 60% and 90% ripe fruit (González-Zamora et al., 2009). However, across their range, spider monkey diets are more varied and diverse than average annual diets suggest, including seasonal instances of feeding on seeds and caterpillars (Cant, 1990), and unripe fruit (Wallace, 2005). Across all study sites, young leaves are the second most common food source, ranging from 21% to 55% of the average annual diet of spider monkeys (reviewed in Gonzalez-Zamora et al. 2009).

Spider monkeys are characterized by high levels of fission-fusion social dynamics (Aureli et al., 2008), and researchers believe these dynamics may have evolved to best exploit the patchy distribution of fruit in the environment. Consequently, research on spider monkey behavioural

ecology has been focused on the relationship between ripe fruit availability and social dynamics. While this research has been critical in understanding spider monkey sociality, focusing on only the primary food source has left the dietary diversity of spider monkeys, and its consequences, relatively unexplored. Folivory, the second most common diet strategy in spider monkeys, has been qualitatively shown to be negatively correlated with fruit availability in some populations (Chapman, 1988; Suarez, 2006), which suggests that leaves may be a fallback food in spider monkeys, but this hypothesis has yet to be tested.

If spider monkeys living in a seasonal environment use leaves as a fallback food in times of low fruit availability there will likely be behavioural consequences extending beyond a simple dietary shift. Morphologically, spider monkeys are unquestionably adapted for a diet high in fruit. Their dental morphology is characterized by well-developed incisors and small molars, both common traits of a highly frugivorous species (Rosenberger, 1992; Rosenberger et al., 2008). Similarly, they have short guts and a low gut passage time, indicating a diet of easily digested food, and their gracile frame and long limbs are hypothesized to have evolved for rapid travel over long distances in pursuit of a patchily distributed food (Cant et al., 2001; Rosenberger et al., 2008). High amounts of suspensory locomotion is an energetically costly form of travel (Parsons and Taylor, 1977), but this strategy is sustainable when ripe fruit is available because of the high levels of lipids and carbohydrates ingested. However, leaves do not contain such high levels of energy (Milton, 1979), which may not be a constraint for species specialized for a diet high in folivory, but could require behavioural adjustments in a species not optimized for extracting nutrients from leaves. Folivorous diets incur more enforced resting time than frugivorous diets (Korstjens et al., 2010), and even on a diurnal scale, spider monkeys follow bouts of leaf-eating

with extended periods of rest (Chapman and Chapman, 1991). On a longer time scale, across a seasonal period of relatively high folivory, spider monkeys may need to maintain a more energy-minimizing strategy (characterized by increased resting and reduced travelling) than they would when fruit is readily available (Wallace, 2005).

Similarly, a period of prolonged folivory in spider monkeys may correlate with social changes. As previously mentioned, the high levels of fission-fusion social dynamics characteristic of *Ateles* are thought to be a response to the patchy availability of ripe fruit (Chapman et al., 1995; Aureli et al., 2008). If this is the case, then periods of leaf-eating, sustained by a comparatively wide-spread and abundant food source, may lead to reduced levels of fission-fusion dynamics characterized by larger subgroups.

Folivory may be used as a fallback strategy in spider monkeys, or it may play a role in nutrient balancing. In Felton et. al's (2009) categorizing of primate nutritional goals, spider monkeys are often thought of as energy-maximizing primates. Researchers have generally built this argument on a combination of theory and morphology: spider monkeys have high levels of daily travel, and a frugivorous (therefore presumably energy-rich) diet. However, few attempts have been made to actually quantify the energy per unit time attained by a foraging spider monkey (but see (Ayala-Orozco et al., 2004), and the categorization of spider monkeys as energy-maximizing primates relies mostly on theory (Strier, 1992). When empirically tested, Felton et al. (2009) found that a population of *Ateles chamek* in Bolivia were not energy maximizing, but instead appeared to choose foods in order to acquire a nutritionally balanced diet, and specifically to maintain a minimum level of daily protein intake.

Study objectives

This study had two objectives. First, I sought to understand the use of fallback foods by a population of black-handed spider monkeys *(Ateles geoffroyi yucatenensis)*, specifically testing the hypothesis that leaves are a fallback food for spider monkeys. If leaves were not a fallback food, they may play a role in nutrient balancing. Second, I explored the behavioural consequences (in terms of monthly activity budgets and average subgroup size) of eating fallback foods, testing the hypothesis that fallback food consumption leads to reduced energy expenditure.

Chapter Two: Methods

Study Site

Data for this study were collected between January 2009 and October 2010 at Runaway Creek Nature Reserve (RCNR), a 2,500 ha private nature reserve in the Belize district of Belize, Central America (88 35'W, 17 22'N). The mean monthly minimum temperature ranges from 16°C in winter to 25°C in summer, and the mean monthly maximum temperature ranges from 28°C in winter to 33°C in summer (Figure 1). Precipitation varies widely across Belize, but in RCNR there is a distinct seasonality, with a wet season from June to December, and a dry season from January to May. Mean annual precipitation around RCNR is approximately 2100 mm, but this may vary on a year-to-year basis (Meerman, 1999).

Runaway Creek is classified into two vegetation zones: tall semi-evergreen broadleaf forest and savannah. Together, these two zones can be further divided into 14 vegetation types (see Meerman 1999 for more detailed discussion). The area is characterized by steep karst hills composed mostly of limestone, and reaching heights of up to 100 m. The karst hills have numerous shallow caves, and the forested valley regions in-between the hills are prone to flooding. Two species of non-human primate inhabit the area: the black howler monkey (*Alouatta pigra*) and the black-handed spider monkey (*Ateles geoffroyi yucatanensis*). The area is also home to potential predators, including the jaguar (*Panthera onca*) and the cougar *(Puma concolor)*. Hurricane Richard hit the field site on October 23rd, 2010, but all of the data analysed here were collected prior to the hurricane.

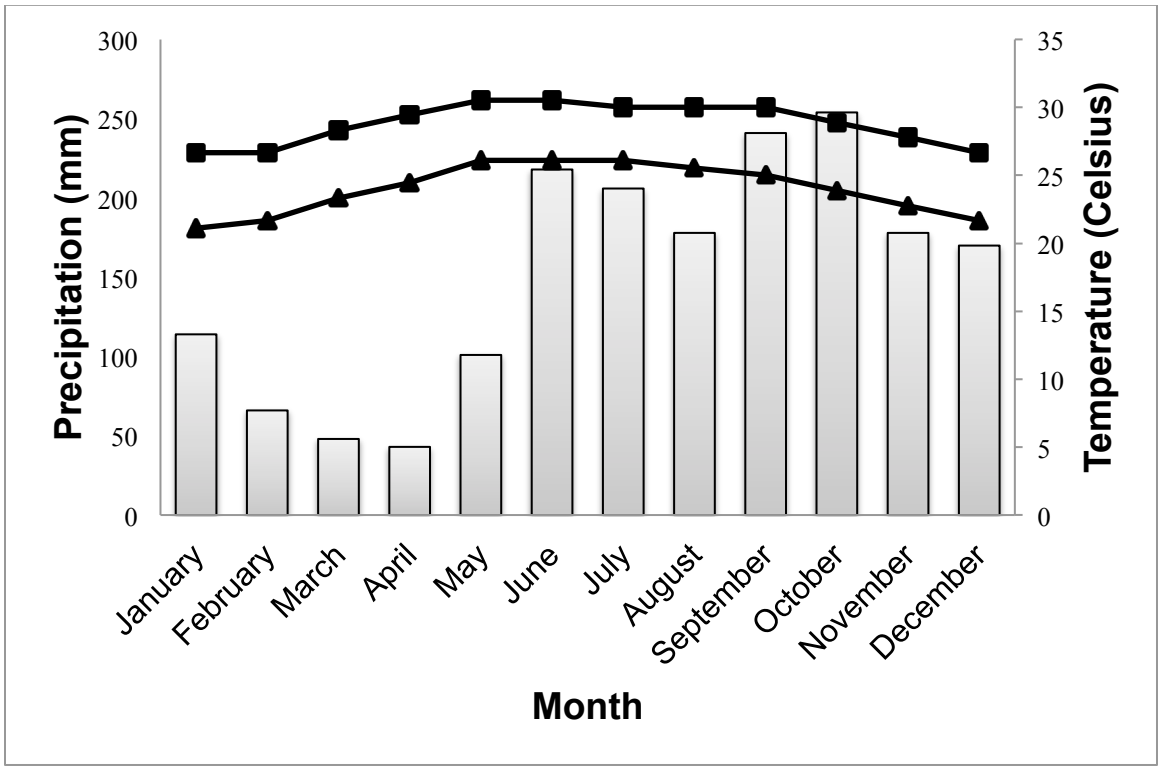

Figure 1. Monthly average precipitation, and minimum and maximum temperatures at Runaway Creek, Belize. Data taken from the Philip S.W. Goldson International Airport weather station, located approximately 50km from the field site.

Study Subjects

Data for this research were collected on one group of *Ateles geoffroyi yucatanensis*. The number of individuals varied between 31 and 37 over the study period (Table 1). All individuals in the group were habituated, and individually recognizable based on facial markings, pelage colour, and skin pigmentation. For the purposes of this study, I considered both adults and sub adults as adults, and did not include infants in the analysis.

Table 1. Composition of a black handed spider monkey group at Runaway Creek, Belize during 2009 and 2010.

Age	**Sex**	**Year**	
		2009	2010
Adult	Male	3	5
	Female	12	13
Sub adult	Male	2	2
	Female	1	2
Juvenile	Male	5	2
	Female	4	6
Infant		8	7
	TOTAL	35	37

Data Collection

Vegetation and environmental data

Researchers collected data on food availability every two weeks in 2009, and monthly in 2010. They walked a phenology trail consisting of 174 marked trees from 34 spider monkey food

species. Over the course of the study two trees died, leaving a final total of 172 trees from 34 species. Between two and fifteen individual trees were assessed for each species, averaging 5.05 individuals/species (Appendix A). The researchers visually assessed the availability of new leaves, mature leaves, flowers, ripe fruit, and unripe fruit, and gave each plant part a score ranging from 0 (no coverage) to 4 (100% coverage). Information on forest structure was collected using 20 vegetation plots, placed randomly throughout the study area, each measuring 40x40 m. Within these plots, researchers measured the diameter-at-breast-height (DBH) for every tree greater than 10 cm, and had them identified by Dr Steven Brewer, a botanist with expertise in the vegetation of Belize.

Behavioural data

Researchers collected data using scan sampling during full- or half-day subgroup follows, four to five days a week (Altmann, 1974). Every 30 minutes, they scanned the subgroup being followed and recorded the group composition and group spread, as well as the individual ID's and behavioural state of all animals present. Possible behavioural states were feeding, inactive, social, or travelling. When individuals were feeding, researchers recorded the plant part and species being fed on; when animals were socializing, researchers recorded the type of social behaviour and the IDs of any interactants (see Ethogram for more details, Appendix B). These scans were used to calculate average monthly activity budgets by dividing the number of scans observed for a specific activity by the total number of scans.

This same process was used to determine monthly diet proportions: the number of scans where individuals were observed feeding on a given plant part was divided by the total number of feeding scans. This method risks inaccuracies in assessing the relative importance of food items, as it can under- or over-estimate the presence of foods in the diet, but overall has been shown to

be valid for studying diet choice in wild non-human primates (Gilby et al. 2010). Data used here were collected between January 2009 and the end of October 2010, resulting in 21 months of observations. December 2009 was excluded from all analyses because no vegetation data were collected during that month.

Data Analyses

Analyses were performed in Stata 12.1 (StataCorp 2011) and R v2.15 (R Foundation for Statistical Computing 2012).

Calculation of plant part availability

Plant part availability was calculated using phenological and vegetation structure data, following Silver et al. (1998) and Brower et al. (1990). First, diameter at breast height (DBH) was converted to basal area for each tree measured. Then the basal areas were summed for each species, giving a total basal area per species. The relative coverage of a species was determined by dividing the total basal area for each species by the total basal area of all measured species.

Phenological scores were averaged for each plant part by species for each measurement period, and then multiplied by the relative coverage of that species to calculate food availability by plant part for each species. The availability of each plant part was summed across all species to give a monthly measure of food availability for each of three plant parts (ripe fruit, leaves, and flowers). The category 'leaves' contained leaf buds and young leaves. Mature and old leaves were not included in the calculations because they were not observed to be eaten by the study group. Unripe fruit was not included, as it was rarely eaten and difficult for researchers to accurately

identify from the ground. In 2009, phenology data was collected twice a month, but in 2010 it was collected only once a month. I averaged the 2009 scores to get one measure per month (N = 21 months). In addition to calculating plant part availability, I also determined the average monthly proportion of trees displaying each phenological phase. All values presented are means plus one standard error.

Modelling plant part selection

I used a multinomial logit model (MNLM) to model plant part selection, using the diet data obtained by scan sampling. MNLM is a technique used to predict the likelihood of an outcome with a categorical dependent variable. It is a generalization of a logistic model, but unlike the logistic model, MNLM allows for more than two possible outcomes. Each scan sample has a number of independent variables attached to it: the individual ID, a ripe fruit availability score, and the age and sex of an individual, and one categorical outcome: the individual was eating fruit, leaves, or flowers. The model uses all of the scans to calculate the probability of each outcome occurring, based on the independent variables. MNLM is commonly used by political scientists to model voter choice, and by epidemiologists to model disease risk, but has also been successfully used by ecologists to model animal diets.

The independent variables included in the model were fruit availability (as determined above), sex (1 = male, 0 = female), age (1 = adult, 0 = juvenile), and individual ID. The dependent variable was plant part selection, modelled as one of three categorical choices: ripe fruit, leaves, or flowers. I used ripe fruit as the reference category, which is the denominator for the calculation of the odds ratio for each category of the dependent variable. The model was built based on 1453 individual feeding records from scan sampling, collected between January 2009

and October 2010, and was bootstrapped 1000 times to provide robust estimates of the coefficients (Sanabila et al 2010).

MNLM relies on the assumption of independence of irrelevant alternatives (IIA). IIA requires that the odds of selecting a particular categorical outcome do not change if a new, irrelevant alternative outcome is added (e.g. the probability of feeding on leaves is not changed if 'hamburger' is added as a new categorical outcome)(Long and Freese 2001). I used the Small-Hsiao test to test the assumption of IIA, and the assumption was met (Table 2) (Small and Hsiao 1985). Following analysis, I used the calculated model coefficients to generate predicted probabilities for each of the four categorical choices (Long and Freese 2001).

Table 2. Small-Hsiao test of the assumption of IIA. The test meets assumptions (all p values are >0.05).

Omitted	**X2**	**df**	**P>X2**
Leaves	8.239	5	0.144
Flowers	5.704	5	0.336
Ripe Fruit	7.27	5	0.201

Modelling the effect of fallback food consumption on activity budgets

The analysis of plant part selection detailed above revealed flowers, but not leaves, to be a fallback food (see Results for details). Subsequently, the remaining analyses of fallback foods use the proportion of flowers consumed per month as an independent variable. Following Lappan (2009), I used a multivariate general linear model (GLM) to analyse the effect of flower eating on activity budgets. I used age, sex, and the monthly proportion of feeding scans spent eating flowers as the independent variables, and the proportion of scans in each of three activities

(feeding, social, travel) as dependent variables. The analysis was performed using 6434 scan samples. These samples were averaged for each of four age-sex classes (adult male, adult female, juvenile male, juvenile female) per month. If a month had less than 20 scan samples for an age-sex class, that class was dropped from the month to avoid the problem of small sample sizes (Martin and Bateson 2007). The model considered all interactions. The full model design was: Flowers + Sex + Age + (Flowers*Sex) + (Flowers*Age) + (Age*Sex) + (Flowers*Age*Sex).

The proportion of time spent inactive did not meet the assumptions of a GLM - it had a non-normal distribution, which could not be transformed to normality. It was analysed separately using non-parametric tests. Mann-Whitney U tests were used to examine the effect of age and sex on inactivity, and a Pearson rank correlation was used to examine the relationship between flower consumption and inactivity.

Modelling the effect of fallback food on subgroup size

To analyse the effects of fallback food consumption on subgroup size, I used a generalized linear model (GLM). I included the average monthly proportion of diet accounted for by feeding on flowers as the fixed effect (flowers were chosen based on the results of the plant part selection model detailed above). The dependent variable was subgroup size. Because subgroup size was collected as count data with a mean <5, I used a Poisson distribution with a log-link function (Bolker et al 2009). The model was based on 1599 scan measurements of subgroup size, which included adults and juveniles of both sexes, but not infants. The calculated coefficients were based on a model bootstrapped 10,000 times to provide robust estimates.

Chapter Three: Results

The results section begins with a brief overview of the diets of the spider monkeys at Runaway Creek Nature Reserve, followed by detailing the plant part availability. I then cover the identification of a fallback food, and the effect of consuming a fallback food on activity budgets and average subgroup size.

Diet overview

The spider monkeys at Runaway Creek consumed ripe fruit in all 21 months of the study period. Ripe fruit made up an average of 61% +/- 4.66% of the monthly diet, ranging from 13.7% in January 2010 to 100% in August 2010. The study population ate the ripe fruit of 65 different species, of which 16 accounted for at least 1% of the total diet over the study period (Table 3). Figs (Ficus *sp.*) made up the largest proportion of the fruit-based diet (25.1%), with three other species each accounting for at least 5% of fruit consumption.

Leaves were eaten in 20 of the 21 study months, and accounted for an average of 23.4% of the monthly diet (ranging from 0% in August 2010 to 46.8% in April 2010). The spider monkeys ate the new leaves of 36 different species. Ten of those species accounted for at least 1% of the total proportion of folivory (Table 4). Similar to fruit eating, figs made up the largest proportion of folivory (39.4%), with two other species accounting for greater than 5%.

Flowers were eaten in 13 out of 21 of the months sampled, and averaged 12% +/- 4.21% of the monthly diet (ranging from 0% in a number of months, to 61.4% in January 2010). In the 13

months in which flowers were consumed, they accounted for an average of 19.4% +/- 6% of the diet (ranging from 0.90% to 61.4%). The spider monkey population ate the flowers of 12 species, but two-thirds of consumption was accounted for by only three species: *Brosimium alicastrum* (47.1%), *Combretum fruticosum* (19.9%) and *Ampelocera hottlei* (10.5%)(Table 5). Flower consumption was highest from January to April in each study year. These months together accounted for 92.1% of all flower consumption observed during the study period (Figure 2).

Table 3. Tree species that accounted for at least 1% of total ripe fruit consumption during the study period, and the proportion of total frugivory for which they were responsible.

Species Name	**Proportion**
Ficus *sp.*	0.251
Manilkara chicle	0.0896
Metopium brownei	0.0768
Attalea cohune	0.0768
Protium copal	0.0512
Caesalpinia gaumeri	0.0448
Spondias radlkoferi	0.0416
Brosimum alicastrum	0.0395
Pseudolmedia spuria	0.0363
Simarouba glauca	0.032
Sabal mauritiiformis	0.032
Trophis racemosa	0.0288
Cissus *sp.*	0.0224
Unknown vine	0.0213
Acacia cookii	0.0203
Philodendron radiatum	0.0192

Table 4. Tree species that accounted for at least 1% of total leaf consumption during the study period, and the proportion of total folivory for which they were responsible.

Species Name	**Proportion**
Ficus *sp.*	0.395
Brosimum alicastrum	0.163
Dialium guianense	0.151
Protium copal	0.0574
Aspidosperma megalocarpon	0.574
Cestrum noctornum/racemosum	0.0215
Unknown	0.0215
Cecropia peltata	0.0191
Ampelocera hottlei	0.0191
Spondias radlkoferi	0.0120

Table 5. Tree species from which spider monkeys ate flowers during the study period, and the proportion of total flower-eating for which each species was responsible.

Species Name	**Proportion**
Brosimium alicastrum	0.471
Combretum fruticosum	0.198
Ampelocera hottlei	0.105
Pseudobombax ellipticum	0.0838
Pseudomedia spuria	0.0419
Drypetes browneii	0.0314
Luhea speciosa	0.021
Trophis racemosa	0.0157
Aspidosperma megalocarpon	0.0157
Sabal yapa	0.00523
Unknown	0.00523
Lonchocarpus rugosus	0.00523

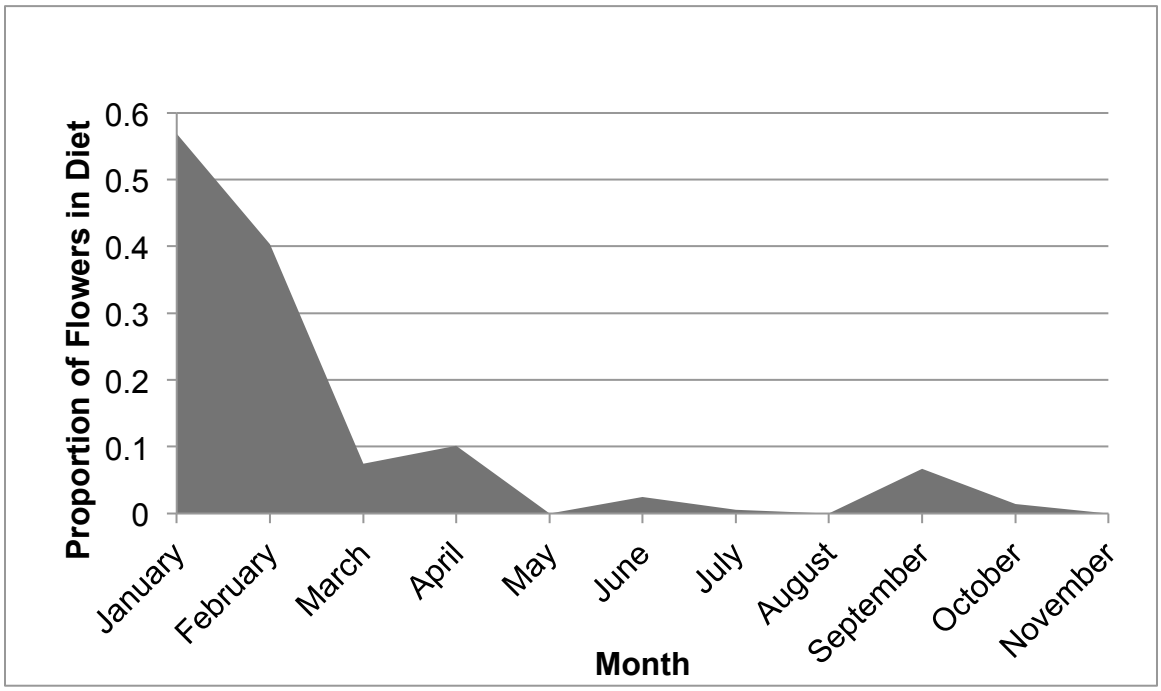

Figure 2. Average monthly flower consumption during 2009 and 2010. Data were not collected in December. The period from January to April accounts for 92.1% of all observed flower consumption during the study period.

Plant part availability

Ripe fruit was present on an average 6.53% of the phenology trees each month, while leaves were present on an average 62.8% and flowers were present on an average 13% of the trees each month (Table 6). Plant part availability varied seasonally at Runaway Creek, but ripe fruit was generally the least available plant part and leaves were usually the most available (Figure 3). Ripe fruit availability peaked in May before declining through late August-January. Statistically, the peaks in ripe fruit availability coincided with peaks in flower availability, and the two food types were significantly positively correlated (pairwise correlation: $r^2 = 0.053$, df = 21, $p<0.05$).

Table 6. Average monthly availability and monthly percent of trees in a phenological phase between January 2009 and October 2010. Based on monthly surveys of 172 trees, presented as means +/- 1 SE.

Plant Part	**Avg Monthly Availability**	**±SE**	**Avg Monthly %**	**±SE**
Ripe Fruit	9.94×10^{-3}	7.56×10^{-3}	6.53	0.967
Leaves	1.05×10^{-1}	9.42×10^{-3}	62.8	4.18
Flowers	3.71×10^{-2}	5.95×10^{-3}	13	1.71

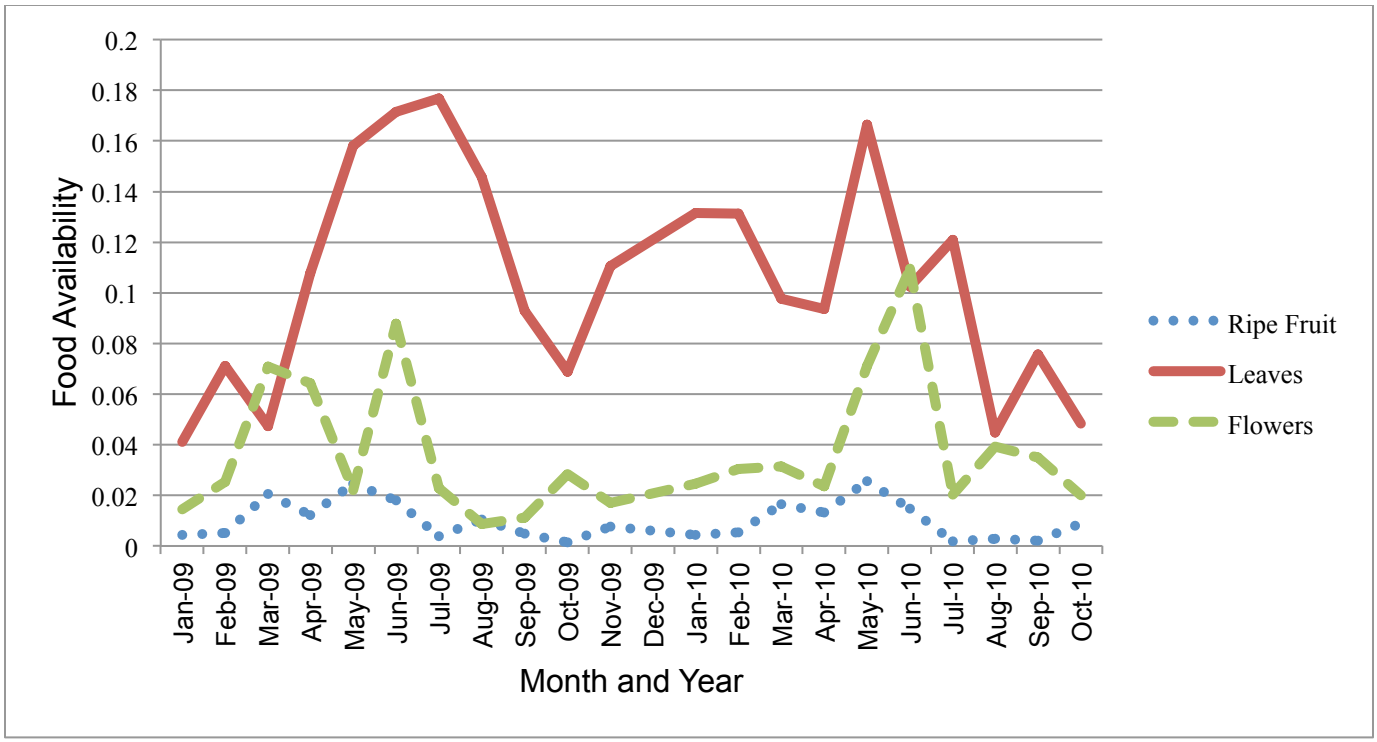

Figure 3. Food availability scores at Runaway Creek between January 2009 and October 2010. Based on monthly phenology scores, calculated from a phenology trail of 172 trees from 34 species.

Plant part selection: flowers as a fallback food

The overall model to determine the effects of age, sex, individual ID and ripe fruit availability on plant part selection returned significant results (MNLM: $X^2 = 132$, df = 8, $p<0.001$). Sex and ripe fruit availability contributed significantly to the model, while age and individual ID did not (Table 7). The bootstrapped coefficients calculated by the model are presented in Table 7.

There was no significant relationship between ripe fruit availability and the log odds of feeding on leaves, indicating that ripe fruit availability did not significantly predict the probability that an individual would feed on leaves ($\beta = -5.765$, CI: −20.7 to 9.355, $p = 0.469$). However, there was a significant relationship between an individual's sex and the probability it would feed on leaves; females were significantly more likely than males to eat leaves ($\beta = -0.289$, CI: −0.581 to −0.014, $p = 0.042$) There was a significant negative relationship between ripe fruit availability and the log odds of feeding on flowers, indicating that the probability of flower consumption was at its highest when fruit was unavailable, and flower consumption decreased as fruit became more available ($\beta = -151$, CI: −186 to −120, $p = 0.001$)(Figure 4)(Figure 5). There was no significant difference between males and females in the probability of flower consumption. Age and individual ID did not have a significant effect on the consumption of any of the measured plant parts (Table 7).

Table 7. Plant part selection model coefficients calculated based on 1453 scan samples collected between January 2009 and October 2010. Coefficients reported here are based on a model bootstrapped 1000 times. Bolded times are significant ($p<0.05$). The independent variables were sex, age, individual ID and ripe fruit availability (RFA). The dependent variable was plant part (flowers, leaves, or ripe fruit). Ripe fruit was the reference category, and therefore is not presented here.

Plant Part	**β**	**Lower**	**Upper**	**Significance**
Leaves				
Sex	-0.289	-0.996	-0.148	**0.042**
Age	-0.188	-0.581	-0.014	0.159
RFA	-5.765	-20.8	9.355	0.469
Individual	0.001	-0.012	0.013	0.823
Flowers				
Sex	-0.346	-0.76	0.042	0.084
Age	-0.256	-0.605	-0.101	0.162
RFA	-151	-186	-120	**0.001**
Individual	0.009	-0.008	0.026	0.286

indicates significance at $p<0.05$.

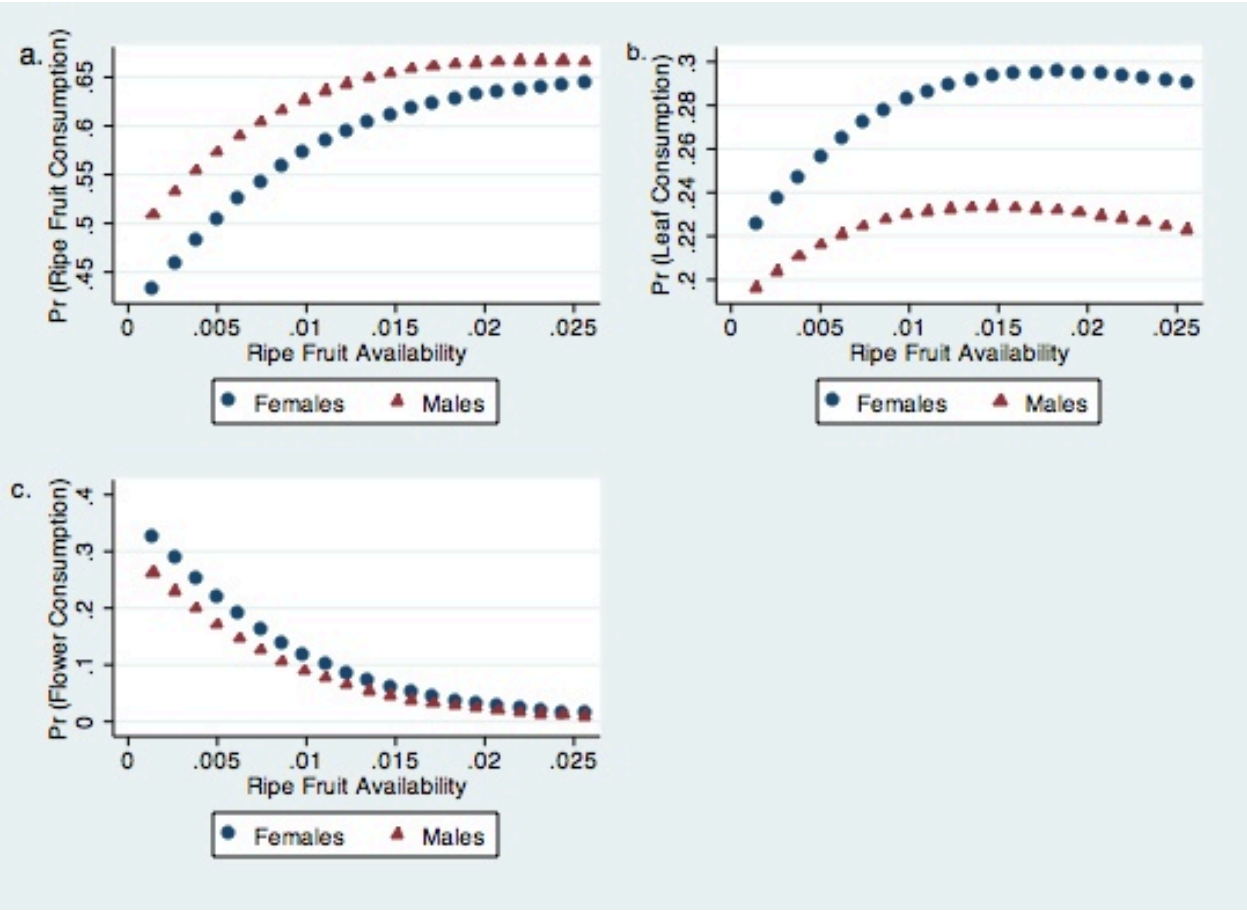

Figure 4. Predicted probabilities of plant part consumption for male and female black-handed spider monkeys at Runaway Creek across a range of ripe fruit availability scores. Females were significantly more likely than males to consume leaves (b, $p < 0.05$). The negative relationship between flower consumption and ripe fruit availability was also significant (c, $p < 0.001$). Based on 1453 scans collected between January 2009 and October 2010.

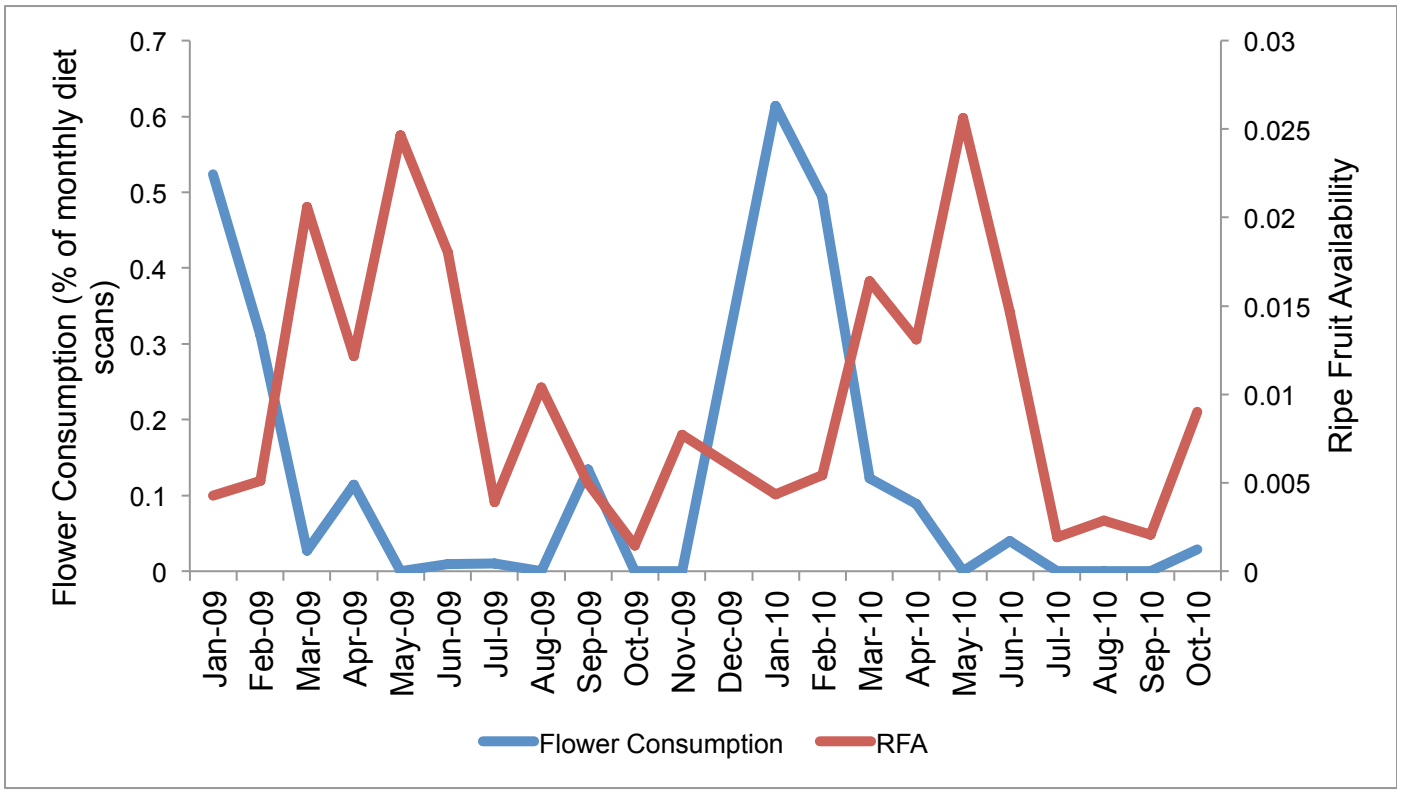

Figure 5. The relationship between flower consumption and ripe fruit availability over 21 months at Runaway Creek, Belize. The relationship is significant: as ripe fruit availability increased, flower consumption decreased significantly ($\beta = -151$, CI: -186 to -120, $p = 0.001$).

The effect of fallback food consumption on monthly activity budgets

To determine the effect of flower consumption on monthly activity budgets I used a multivariate GLM, with flower consumption, age, and sex as independent variables and proportion of scans spent feeding, socializing, and travelling as dependent variables. Sex did not have a significant effect on the proportion of time spent in any activity (Table 8). Age significantly affected the proportion of time spent socializing ($F = 4.836$, df = 1,20, $p = 0.040$); juveniles socialized significantly more than did adults (a category including social grooming and social play). Age did not significantly affect any other activities (Table 8).

The proportion of flowers in a monthly diet significantly affected the proportion of scans spent feeding ($F = 3.269$, df = 13,20, $p = 0.009$) and the proportion of scans spent travelling ($F = 5.381$, df = 13, 20, $p = 0.000$), but not the proportion of scans spent socializing ($F = 1.302$, df = 13, 20, $p = 0.289$). Increased flower eating led to a significant increase in the amount of feeding (Figure 6), and a significant decrease in the amount of travelling (Figure 7). There was a significant interaction between sex and age in the proportion of scans spent travelling ($F = 14.147$, df = 1,20, $p = 0.001$): adult males travelled significantly more than other age-sex classes. No other interactions were significant. The full table of results is available in Appendix C. The proportion of time spent inactive was examined using non-parametric tests. It did not vary by age (Mann-Whitney U: U = 472, N = 69, $p = 0.141$), sex (Mann-Whitney U: U = 457, N = 69, $p = 0.121$), or with the consumption of flowers (Pearson rank correlation: $r = -0.085$, N = 69, $p = 0.486$)

Table 8. Main effect results for a GLM with flower consumption, sex, and age as independent variables and the proportion of scans spent feeding, socializing, and travelling as the dependent variables. Based on data collected between January 2009 and October 2010. N = 69 age-sex class/month categories. Interactions were largely non-significant, and so are excluded here. The complete model table can be found in Appendix C.

Effect	**F**	**df**	**Significance**
Flowers			
Feed	3.269	13	**0.009**
Social	1.302	13	0.289
Travel	5.381	13	**0.000**
Sex			
Feed	0.01	1	0.921
Social	0.441	1	0.514
Travel	0.252	1	0.621
Age			
Feed	1.142	1	0.298
Social	4.836	1	**0.04**
Travel	0.089	1	0.769

indicates significance at $p < 0.05$.

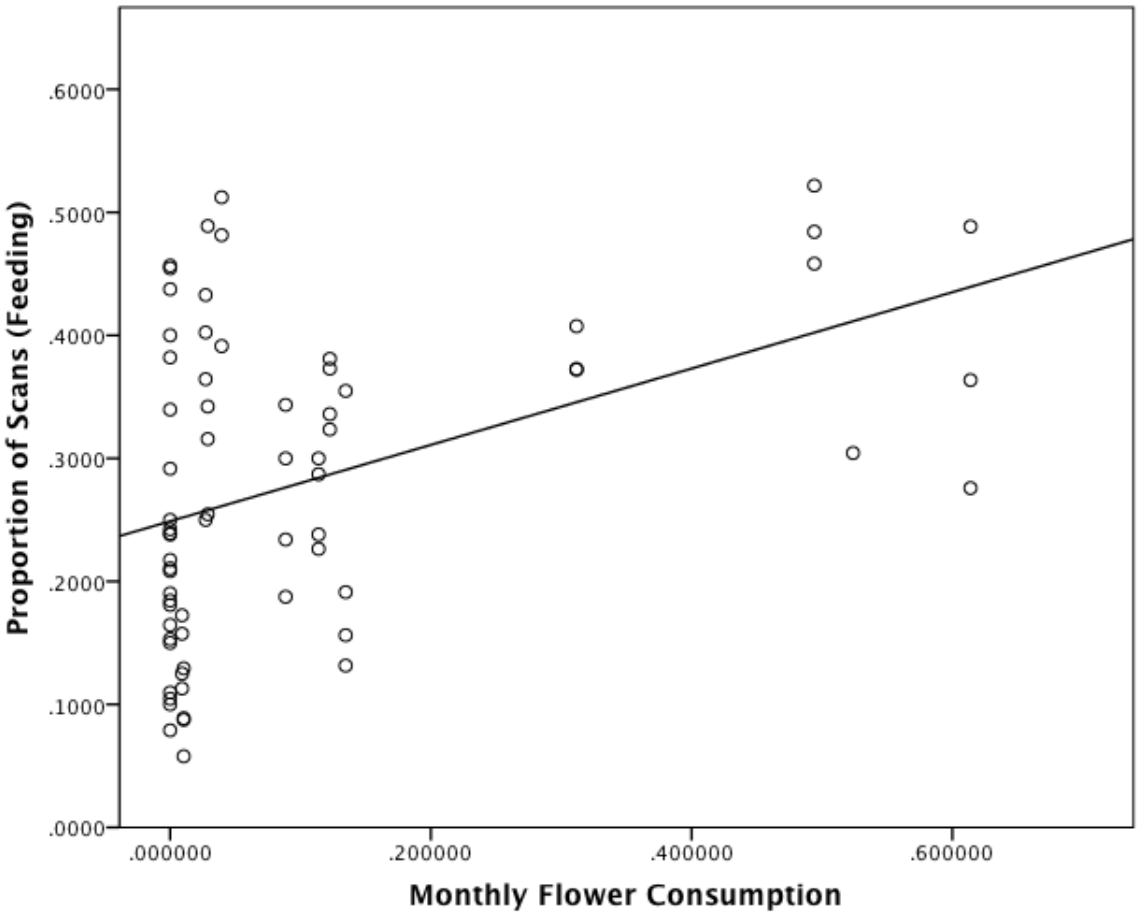

Figure 6. The relationship between feeding and monthly flower consumption for the spider monkeys at Runaway Creek. The relationship is significant ($F = 3.269$, $df = 13,20$, $p = 0.009$). As flower consumption increased, so did the proportion of time spent feeding.

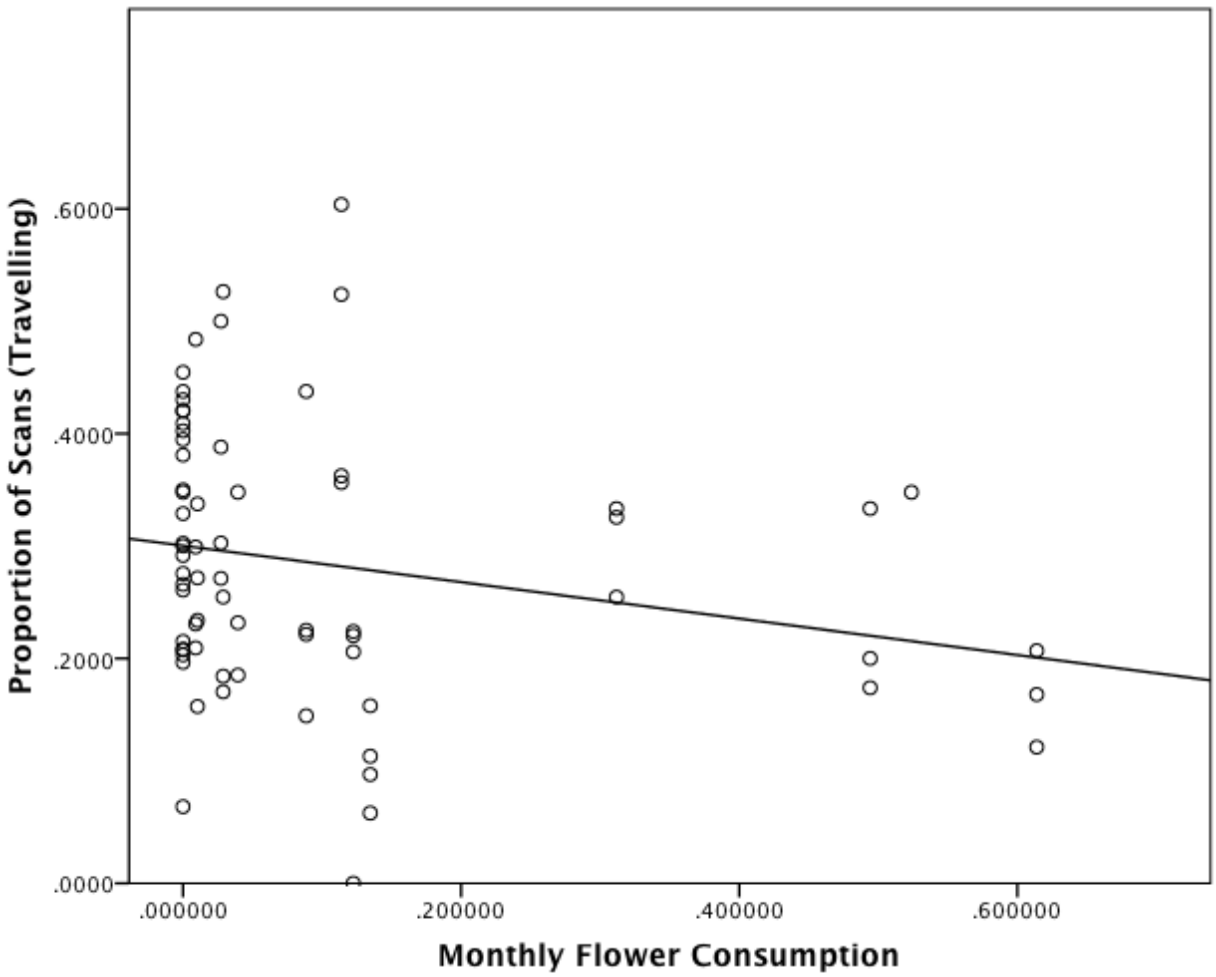

Figure 7. The relationship between travelling and monthly flower consumption. The relationship is significant (F = 5.381, df = 13,20, p = 0.000). As flower consumption increased, the proportion of time spent travelling decreased.

The effect of fallback food consumption on subgroup size

The mean subgroup size of the spider monkeys at Runaway Creek was 4.44 individuals (+/- 0.076). Subgroup size ranged between 1 and 22 individuals. The most frequently observed subgroup size was two individuals (Figure 8). The generalized linear model used to determine the effect of fallback foods on group size was significant (generalized linear model: z = −12.25, CI: −1.470 - (-1.064), p = 0.000); as flower eating increased, subgroup size decreased significantly (Figure 9).

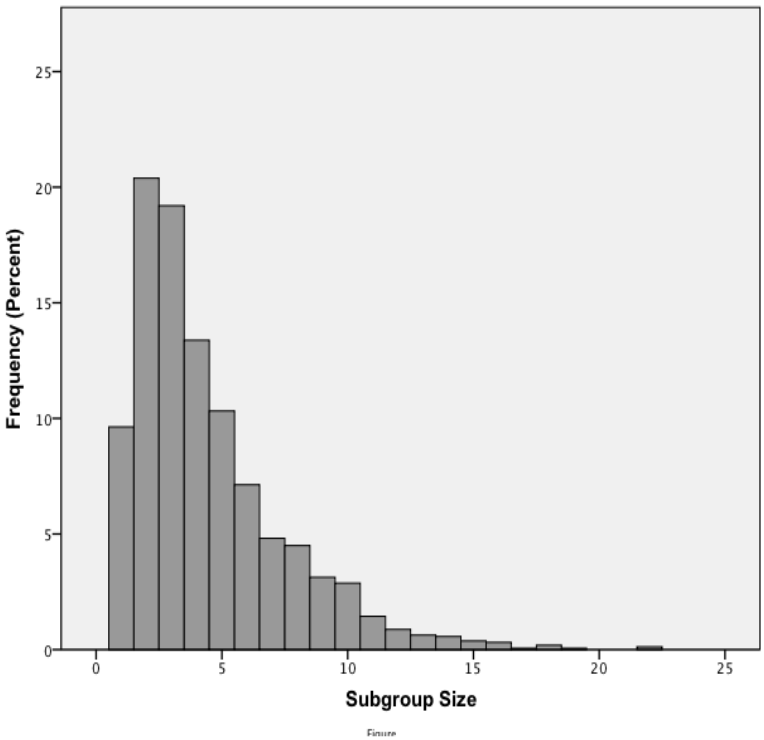

Figure 8. Frequency of subgroup sizes observed at Runaway Creek, based on 1599 scan samples of subgroups. The most frequent subgroup size was two individuals, and the mean was 4.44 individuals.

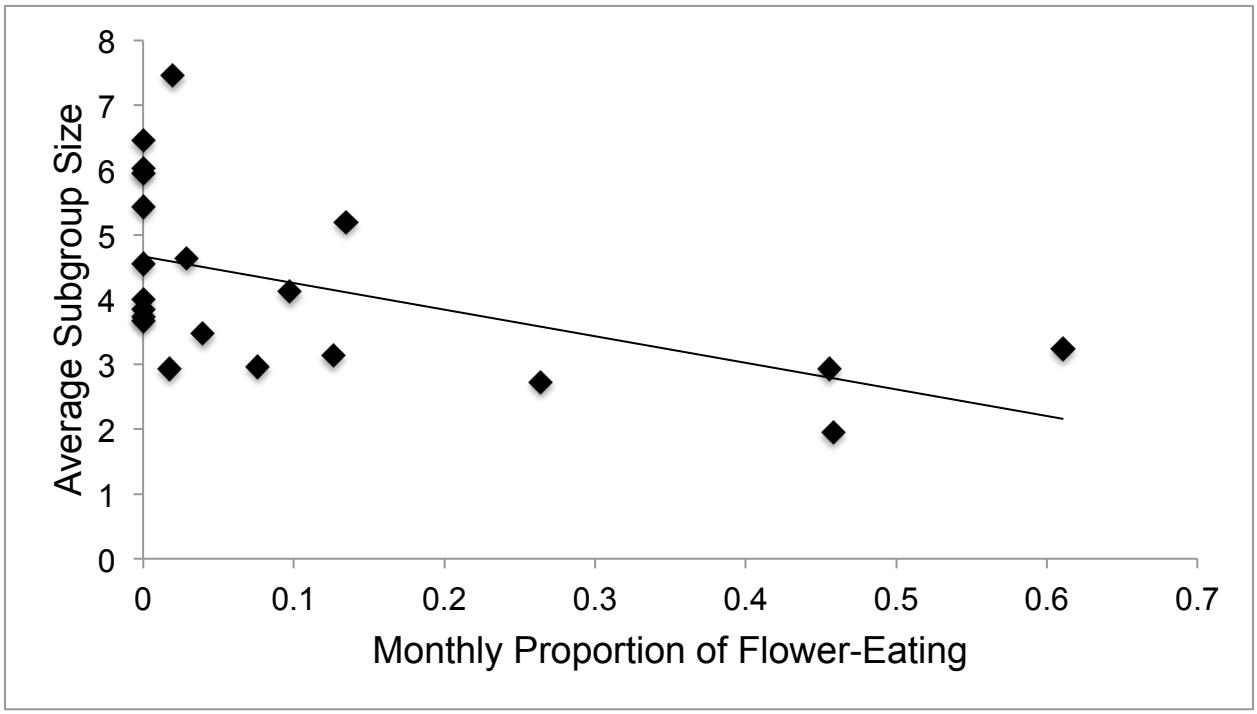

Figure 9. The relationship between average monthly subgroup size and the proportion of flowers in the diet. The relationship was significant (generalized linear model: $z = -12.25$, $p = 0.000$). As the proportion of flowers in the diet increased, the average subgroup size decreased.

Chapter Four: Discussion

Folivory in spider monkeys at Runaway Creek

Folivory was not a fallback strategy for the spider monkeys at Runaway Creek: the consumption of leaves did not vary significantly with changes in the availability of ripe fruit. This result differs from research at a few other spider monkey populations, which have found that folivory increases during periods of fruit scarcity. A study on black spider monkeys *(Ateles chamek)* in Bolivia found that during months of relatively low fruit availability, individuals increased their folivory (Wallace, 2005). This was attributed to the specific feeding behaviour of this study population: for most of the year, they rely heavily on a small number of keystone species with fruiting patterns that do not overlap. Therefore, preferred food is almost always available - except in one month, where the spider monkeys rely heavily on leaves (Wallace, 2005). The spider monkeys at Runaway Creek do not rely heavily on particular fruit species (with the exception of figs), so there may not be a time period where leaves are their only food choice.

Leaf-eating at Runaway Creek was not a fallback strategy, but leaves may be a staple food source. Folivory accounted for an average of 23.4% of the annual diet for all individuals, which is not markedly higher than the 21% average across spider monkey populations (González-Zamora et al., 2009). Nor was the monthly range different: 0-46.8% at Runaway Creek, versus 0-55% across spider monkey study sites (González-Zamora et al., 2009). The main difference then appears to be that folivory at Runaway Creek is less seasonal: the spider monkeys are eating similar amounts of leaves to other study sites, but not localizing that folivory to periods of low fruit availability. Consistent folivory suggests that leaves are being used as a staple food, possibly in the interest of nutrient balancing (Felton et al., 2009a; c). However, future research

measuring nutrient intake and energy balance is needed to determine if folivory is being used as a way of nutrient balancing.

Why are females more likely to eat leaves?

At Runaway Creek, female black-handed spider monkeys were significantly more likely than males to consume leaves, across a range of ripe fruit availabilities (Figure 3). This pattern has not been reported statistically in any other spider monkey population (Suarez 2006 reports a difference in folivory between males and females, but it is not tested statistically). However, the result is not uncommon across other nonhuman primate species, both guenons (*Cercopithecus* spp.) (Gautier-Hion, 1980; Cords, 1986; Nakagawa, 2000), and patas monkeys (*Erythrocebus patas*) (Nakagawa, 2000) show higher amounts of folivory in females than in males.

The most likely proposed explanation is differences between the sexes in energetic and nutritional requirements (although other explanations, including the influence of female-directed male aggression at feeding sites, and male sexual strategies, have also been proposed. See Koenig 2002). Females may eat more leaves because the energetic demands of lactation and parturition drive an increased need for a more proteinaceous diet compared to males (Gautier-Hion, 1980; Cords, 1986; Key and Ross, 1999; Nakagawa, 2000). Pregnancy increases females energetic and protein demands by up to 25%, and lactation increases those demands by up to 50% (Coelho, 1974; Key and Ross, 1999; Dias et al., 2011). Meeting these protein demands may be difficult for tropical frugivores (Courts, 1998; Felton et al., 2009a), and the costs of protein deficiency during gestation can be high, including increased infant mortality, and reduced birth weight and growth rate (Riopelle et al., 1974; Fleagle et al., 1975; Riopelle et al., 1975). For an

tropical herbivore, the most readily available source of biologically accessible protein is young leaves (Milton, 1984; Ruby, 2000; Milton, 2006). The higher leaf consumption observed in female spider monkeys may be a way of increasing protein intake to meet the demands of gestation and lactation particularly as spider monkeys may nurse infants for upwards of two years (Milton 1981).

Falling back on flowers

Eating flowers appears to be a fallback strategy for the spider monkeys at Runaway Creek: as the availability of ripe fruit decreased, the chance of eating flowers increased significantly. Flower-consumption led to significant increases in the proportion of time spent feeding, decreases in the proportion of time spent travelling, and a decrease in average subgroup size. This is the first time flowers have been suggested as a fallback food for a population of spider monkeys.

Flower consumption at Runaway Creek was highly seasonal. Flowers were heavily consumed January through April (92.1% of all flowers consumed during the study period were eaten during these months), and were rarely eaten during the summer (May through August) when ripe fruit was abundant. Monthly flower consumption ranged from 0% in a number of summer months, to 61.4% of the diet in January 2009, higher then has been reported for other populations of spider monkeys. In a review of studies on spider monkey diets, Gonzalez-Zamora et al. (2009) report that flowers comprise between 1.3% and 7.9% of an annual diet, and between 0% and 29% of monthly diets. However, flower-eating has not been investigated in detail at other sites, so it is possible that interesting patterns of use are present, but not yet documented - a possible

consequence of flowers being treated as a comparatively unimportant food category in nonhuman primates (Lappan, 2009; Lambert, 2011).

While flowers have not been previously identified as a fallback food in spider monkeys, their consumption has been investigated in other frugivorous primates. Siamangs *(Symphalangus syndactylus)* (Lappan, 2009), hybrid Bornean gibbons *(H. muelleri x agilis/albibarbis)* (McConkey et al., 2003), and Bornean orangutans *(Pongo pygmaeus)* (Knott, 1998) all appear to use flowers as a fallback food in times of decreased fruit availability. Like the spider monkeys in this study, these other species appear to favour specific species. The majority of flower consumption at Runaway Creek is accounted for by three species: *Brosimium alicastrum* (47.1% of all flower consumption), *Combretum fruticosum (*19.8%), and *Ampelocera hottlei* (10.5%). This is low dietary diversity, given that at Runaway Creek, the study population consumes the fruit of at least 65 species, and only Ficus *sp*. accounts for greater than 10%. Further analysis of the flower eating at this site should focus on the nutritional composition and availability of these species.

Why flowers? No nutritional analysis of flowers was performed in this study, however, other studies of nonhuman primate diets have discovered that flowers are nutritionally similar to ripe fruit, with the two food types having approximately equal amounts of sugar and fat content (McCabe and Fedigan, 2007). Protein content in flowers varies widely, between 13% and 33% dry mass (McCabe and Fedigan, 2007; Simmen et al., 2007), but is at least equal-to, if not higher than, the protein content of ripe fruit (McConkey et al., 2003; Simmen et al., 2007). When fruit is unavailable flowers are a nutritionally similar substitute. In some frugivorous primates, the

additional protein of flowers compared to fruit may actually make flowers a preferred food source (McConkey et al., 2003).

The effects of flower eating on activity budgets and subgroup size

The spider monkeys at Runaway Creek altered their activity patterns during periods of flower-eating by increasing the proportion of time spent feeding, decreasing time spent travelling, and aggregating in smaller subgroups. These three behaviours can be read as a response to the costs incurred by a diet consisting of flowers. The volume of nectar secreted by tropical flowers on a daily basis ranges from under 10 ul in bee-pollinated species (Perret et al., 2001) to upwards of 20,000 ul in bat-pollinated species (Tschapka 2004), with bird-pollinated species containing intermediate volumes of nectar (McDade and Weeks, 2004). Compared to the mass of a ripe fruit pulp, flowers provide less energy per-capita than does fruit (Hodges, 1981; Schaefer et al., 2002). Nectar volume was not collected for this study, but of the three most commonly consumed flower species one is insect-pollinated *(Brosimum alicastrum)* (Hamrick et al., 1993), and one is bird-pollinated *(Combretum fruticosum)* (Gryj et al., 1990). The third, *Ampelocera hottlei*, comes from a family (Ulmaceae) whose species are either insect- or wind-pollinated (Momose et al 1998). These pollination syndromes suggest that the flowers being eaten at Runaway Creek contain low volumes of nectar.

Compounding the problem of low volumes, nectar is also a dilute solution. While the dry mass of nectar is comparable in nutritional composition to ripe fruit (McCabe and Fedigan, 2007), in tropical flowers up to 50% of nectar volume is water (Wolff, 2006). The study population at Runaway Creek may have increased the time they spent feeding during flower-heavy periods in

order to compensate for the decreased per-capita energy acquired when compared to feeding on ripe fruit. Increases in the proportion of time spent feeding are a common response to fallback foods that differ in nutritional quality or quantity from preferred foods (Marshall and Wrangham, 2007; Altmann, 2009; Vogel et al., 2009), and is a result found in other frugivorous primates falling back on flowers (Lappan, 2009).

A second common behavioural response to feeding on fallback foods, in conjunction with increased feed time, is a decrease in the proportion of time spent travelling (Altmann, 2009; Enari and Sakamaki-Enari, 2013). Together these constitute a "risk-averse" activity budget: decreasing travel reduces unnecessary energy expenditure, and increasing feeding raises the intake of energy (Enari and Sakamaki-Enari, 2013). The spider monkeys at Runaway Creek significantly decreased the time spent travelling as they increased the proportion of flowers in their diet. Given the probable low per-capita energy of flowers (Hodges, 1981; Schaefer et al., 2002), reducing travel may be a risk-averse, energy minimizing strategy (although this does not eliminate the possibility that flower patches may be larger than fruit patches, reducing the need to travel frequently). This outcome is similar to Lappan (2009), who found that siamangs reduced daily path length while feeding on flowers.

Flowers, like fruit, are patchily distributed in the environment: the timing and duration of their flowering can vary dramatically within a community (Bawa et al., 2003). This distribution creates a monopolizable resource, inviting contest competition (Wrangham, 1979; 1980; Sterck et al., 1997). For flowers to be a reliable fallback food, there must be some way of mitigating feeding competition at flowering trees - particularly given the reduced per-capita energy of a

flower compared to a fruit. The high levels of fission-fusion social dynamics present in spider monkeys may provide a mechanism for reducing competition. High levels of fission-fusion dynamics are presumed to be an adaptation for coping with fluctuations in the availability of patchily distributed food (Symington, 1990; Chapman et al., 1995; Aureli et al., 2008). Previously, the size of spider monkey subgroups has been thought to change in accordance with the availability of fruit patches: more fruit, larger subgroups; less fruit, smaller subgroups. However, the results of this study suggest that a second factor, the availability and distribution of fallback foods, also influences subgroup size. Increased reliance on flowers at Runaway Creek was correlated with a significant reduction in average subgroup size, presumably as a mechanism for reducing contest competition at flowering trees.

Where do flowers fit in the fallback food frameworks?

According to the fallback food framework proposed by Lambert (2007), flowers are a high nutritional density food. The nutrition available in flowers does not differ considerably from that available in ripe fruit, spider monkeys' preferred food, and eating flowers does not require specialized morphology. Flowers, like fruit, are patchily distributed, but because of their smaller size, the per-capita nutritional gain from a flower is likely lower, meaning behavioural changes may be required to maintain a continuous level of nutrient intake. In the study population, these behavioural changes took the form of increasing feeding time, decreasing travel time, and decreasing average subgroup size.

Flower-eating fits just as easily into the framework proposed by Marshall and Wrangham (2009). Flowers are not eaten year-round, and never account for 100% of the diet, eliminating them as

staple fallback foods. However, they do fill the role of filler fallback foods: being eaten as a supplementary food source when preferred foods are rare, and being ignored when preferred foods are abundant. Flowers, then, fit best as a high nutritional density, filler fallback food.

Directions for Future Research

For the population of spider monkeys at Runaway Creek, flowers are a high nutritional density filler fallback food. The novelty of this result, thus far unreported at other spider monkey research sites, highlights the importance of considering all foods in a primate's diet when studying their behavioural ecology, and not consigning minor food items solely to the status of "other" (Lappan, 2009; Lambert, 2011). Because the data used for this study were collected before a chain of major disturbances (a hurricane in 2010 and a fire in 2011), the first step in ongoing research should be to determine if the diet habits of the spider monkey population have since returned to their pre-disturbance state. Specifically, future research should begin by determining whether or not flowers are still being used as a fallback food in the low-fruit season between January and April. If flower consumption is continuing, then food samples should be collected and analysed for nutritional content - flowers, but also fruit and leaves. Additionally, studies comparing ingestion rate of flowers vs fruit and other food items should be conducted. With the recent advances made in nutritional ecology, it would also be useful to study fluctuations in the study individuals' energy balance through both the flower-eating and fruit-eating periods of the year: does the increased feeding time during the flower-eating period actually compensate for the decreased per-capita energy of flowers?

With data from this field site now spanning nearly six years, a longitudinal study examining dietary changes should also be conducted. Of specific interest is fluctuation in the use of fallback foods. Fallback foods are context-dependent - what is used as a fallback food depends on the relative availability and value of all other available food types. In this study, flowers were used as a fallback food: they were more available than fruit, and presumably more valuable than leaves. However, during the period immediately following Hurricane Richard, the spider monkey population increased their consumption of leaves - possibly because flowers and fruit were equally unavailable (Champion, *pers. com.*). A long-term study, using pre-disturbance, mid-disturbance, and post-disturbance data could show context-dependent changes in the choice of food, based on the relative availability and value of food types in the environment.

Nonhuman primates have been suggested to be ecosystem engineers - species that modify the abiotic and biotic structure of their environments in sometimes extreme ways (Jones et al., 1994; 2010) - by dispersing seeds and stripping bark from trees to the extent that the tree dies (Chapman et al., 2013). High intensity flower consumption for brief periods of time may fall under this umbrella. Flower-consumption can significantly reduce the reproductive potential of plants (Riba-Hernandez and Stoner, 2005), and the long-term effects of intensive, seasonal flower consumption on forest composition could be significant.

Literature Cited

Altmann J. 1974. Observational Study of Behavior: Sampling Methods. Behaviour 49:227–266.

Altmann SA. 2009. Fallback foods, eclectic omnivores, and the packaging problem. Am. J. Phys. Anthropol. 140:615–629.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, et al. 2008. Fission-Fusion Dynamics. Current Anthropology 49:627–654.

Ayala-Orozco B, Cocho G, Larralde H, Ramos-Fernandez G, Mateos JL, and Miramontes O. 2004. Levy walk patterns in the foraging movements of spider monkeys *(Ateles geoffroyi)*. Behav Ecol Sociobiol 55:223–230.

Bawa KS, Kang H, and Grayum MH. 2003. Relationships among time, frequency, and duration of flowering in tropical rain forest trees. American Journal of Botany 90:877–887.

Behie AM, and Pavelka MSM. 2012a. The Role of Minerals in Food Selection in a Black Howler Monkey *(Alouatta pigra)* Population in Belize Following a Major Hurricane. Am. J. Primatol. 74:1054–1063.

Behie AM, and Pavelka MSM. 2012b. Food selection in the black howler monkey following habitat disturbance: implications for the importance of mature leaves. J. Trop. Ecol. 28:153–160.

Cant JGH, Youlatos D, and Rose MD. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and nonsuspensory modes. Journal of Human Evolution 41:141–166.

Cant JGH. 1990. Feeding ecology of spider monkeys *(Ateles geoffroyi)* at Tikal, Guatemala. Human Evolution 5:269–281.

Chancellor RL, Rundus AS, and Nyandwi S. 2011. The Influence of Seasonal Variation on Chimpanzee *(Pan troglodytes schweinfurthii)* Fallback Food Consumption, Nest Group Size, and Habitat Use in Gishwati, a Montane Rain Forest Fragment in Rwanda. Int J Primatol 33:115–133.

Chapman C, and Chapman L. 1991. The Foraging Itinerary of Spider Monkeys: When to Eat Leaves? Folia Primatol 56:162–166.

Chapman CA, and Pavelka MSM. 2004. Group size in folivorous primates: ecological constraints and the possible influence of social factors. Primates 46:1–9.

Chapman CA, Bonnell TR, Gogarten JF, Lambert JE, Omeja PA, Twinomugisha D, Wasserman MD, and Rothman JM. 2013. Are Primates Ecosystem Engineers? Int J Primatol 34:1–14.

Chapman CA, Wrangham RW, and Chapman LJ. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70.

Chapman CA. 1988. Patterns of foraging and range use by three species of neotropical primates. Primates 29:177–194.

Coelho AM Jr. 1974. Socio-bioenergetics and sexual dimorphism in primates. Primates 15:263–269.

Conklin-Brittain NL, Wrangham RW, and Hunt KD. 1998. Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance. II. Macronutrients. Int J Primatol 19:971–998.

Constantino PJ, and Wright BW. 2009. The importance of fallback foods in primate ecology and evolution. Am. J. Phys. Anthropol. 140:599–602.

Cords M. 1986. Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus Ascanius* and *C. Mitis*. The Journal of Animal Ecology 55:811–827.

Courts SE. 1998. Dietary strategies of Old World Fruit Bats (Megachiroptera, Pteropodidae): how do they obtain sufficient protein? Mammal Review 28:185–194.

Dias PAD, Rangel-Negrín A, and Canales-Espinosa D. 2011. Effects of lactation on the time-budgets and foraging patterns of female black howlers *(Alouatta pigra)*. Am. J. Phys. Anthropol. 145:137–146.

Doran D. 1997. Influence of Seasonality on Activity Patterns, Feeding Behavior, Ranging, and Grouping Patterns in Taï Chimpanzees. Int J Primatol 18:183–206.

Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, and Shah N. 2002. Western lowland gorilla diet and resource availability: New evidence, cross-site comparisons, and reflections on indirect sampling methods. Am. J. Primatol. 58:91–116.

Enari H, and Sakamaki-Enari H. 2013. Influence of Heavy Snow on the Feeding Behavior of Japanese Macaques *(Macaca Fuscata)* in Northern Japan. Am. J. Primatol.:n/a–n/a.

Felton AM, Felton A, Lindenmayer DB, and Foley WJ. 2009a. Nutritional goals of wild primates. Functional Ecology 23:70–78.

Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Wallis IR, and Lindenmayer DB. 2009b. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology 20:685–690.

Felton AM, Felton A, Wood JT, and Foley WJ. 2009c. Nutritional Ecology of *Ateles chamek* in lowland Bolivia: How Macronutrient Balancing Influences Food Choices. Int J Primatol 30:675–696.

Fleagle JG, Samonds KW, and Hegsted DM. 1975. Physical growth of cebus monkeys, *Cebus*

albifrons, during protein or calorie deficiency. The American Journal of Clinical Nutrition 28:246–253.

Ganas J, Ortmann S, and Robbins MM. 2008. Food preferences of wild mountain gorillas. Am. J. Primatol. 70:927–938.

Gautier-Hion A. 1980. Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys. The Journal of Animal Ecology 49:237–269.

Gilby IC, Pokempner AA, and RW Wrangham. 2010. A direct comparison of scan and focal sampling methods for measuring wild chimpanzee behaviour. Folia Primatol. 81:254-264.

Goldsmith ML. 1999. Ecological Constraints on the Foraging Effort of Western Gorillas *(Gorilla gorilla gorilla)* at Bai Hokōu, Central African Republic. Int J Primatol 20:1–23.

González-Zamora A, Arroyo-Rodríguez V, Chaves ÓM, Sánchez-López S, Stoner KE, and Riba-Hernández P. 2009. Diet of spider monkeys *(Ateles geoffroyi)* in Mesoamerica: current knowledge and future directions. Am. J. Primatol. 71:8–20.

Grueter CC, Li D, Ren B, Wei F, Xiang Z, and van Schaik CP. 2009. Fallback foods of temperate-living primates: A case study on snub-nosed monkeys. Am. J. Phys. Anthropol. 140:700–715.

Gryj E, del Rio CM, and Baker I. 1990. Avian Pollination and Nectar Use in *Combretum fruticosum* (Loefl.). Biotropica 22:266–271.

Hamrick JL, Murawski DA, and Nason JD. 1993. The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. Vegetatio 107/108:281–297.

Herrera G, Gutierrez E, Hobson K, Altube B, Diaz WG, and Sanchez-Cordero V. 2002. Sources of assimilated protein in five species of New World frugivorous bats. Oecologia 133:280–287.

Hodges CM. 1981. Optimal foraging in bumblebees: hunting by expectation. Anim. Behav. 29: 1166-1171.

Jones CG, Gutiérrez JL, Byers JE, Crooks JA, Lambrinos JG, and Talley TS. 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119:1862–1869.

Jones CG, Lawton JH, and Shachak M. 1994. Organisms as Ecosystem Engineers. Oikos 69:373–386.

Key C, and Ross C. 1999. Sex differences in energy expenditure in non–human primates. Proceedings of the Royal Society B: Biological Sciences 266:2479–2485.

Knott CD. 1998. Changes in Orangutan Caloric Intake, Energy Balance, and Ketones in Response to Fluctuating Fruit Availability. Int J Primatol 19:1061–1079.

Knott CD. 1999. Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability.

Knott CD. 2005. Energetic responses to food availability in the great apes: Implications for Hominin Evolution. In: Brockman DK, Van Schaik C, editors. Primate Seasonality: Implications for Human Evolution. Cambridge University Press. p 351–378.

Koenig A. 2002. Competition for Resources and Its Behavioral Consequences Among Female Primates. Int J Primatol. 23: 759-783.

Korstjens A, Lehmann J, and Dunbar R. 2010. Resting time as an ecological constraint on primate biogeography. Anim Behav 79:361–374.

Krishnadas M, Chandrasekhara K, and Kumar A. 2011. The response of the frugivorous lion-tailed macaque *(Macaca silenus)* to a period of fruit scarcity. Am. J. Primatol. 73:1250–1260.

Lambert J. 2007. Seasonality, Fallback Strategies, and Natural Selection: A Chimpanzee and Cercopithecoid Model for Intrepreting the Evolution of Hominin Diet. In: Ungar P, editor. Evolution of the Human Diet: The Known, the Unknown, and the Unknowable. 1st ed. New York: Oxford University Press. p 324–343.

Lambert J. 2011. Primate Nutritional Ecology: Feeding Biology and Diet at Ecological and Evolutionary Scales. In: Campbell C, Fuentes A, MacKinnon K, Bearder S, Stumpf R, editors. Primates in Perspective. 2nd ed. New York: Oxford University Press. p 512–522.

Lambert JE, Chapman CA, Wrangham RW, and Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. Am. J. Phys. Anthropol. 125:363–368.

Lappan S. 2009. Flowers are an important food for small apes in southern Sumatra. Am. J. Primatol. 71:624–635.

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

Liem KF. 1973. Evolutionary Strategies and Morphological Innovations: Cichlid Pharyngeal Jaws. Systematic Zoology 22:425–441.

Liem KF. 1990. Aquatic Versus Terrestrial Feeding Modes: Possible Impacts on the Trophic Ecology of Vertebrates. Integr Comp Biol 30:209–221.

Marshall AJ, and Wrangham RW. 2007. Evolutionary Consequences of Fallback Foods. Int J Primatol 28:1219–1235.

Marshall AJ, Boyko CM, Feilen KL, Boyko RH, and Leighton M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. Am. J. Phys. Anthropol. 140:603–614.

Mattson WJ Jr. 1980. Herbivory in Relation to Plant Nitrogen Content. Annual review of ecology and systematics 11:119–161.

McCabe GM, and Fedigan LM. 2007. Effects of Reproductive Status on Energy Intake, Ingestion Rates, and Dietary Composition of Female *Cebus capucinus* at Santa Rosa, Costa Rica. Int J Primatol 28:837–851.

McConkey KR, Ario A, Aldy F, and Chivers DJ. 2003. Influence of Forest Seasonality on Gibbon Food Choice in the Rain Forests of Barito Ulu, Central Kalimantan. Int J Primatol 24:19–32.

McDade LA, and Weeks JA. 2004. Nectar in Hummingbird-pollinated Neotropical Plants I: Patterns of Production and Variability in 12 Species. Biotropica 36:196–215.

Meerman JC. 1999. Rapid Ecological Assessment: Runaway Creek, Belize. Foundation for Wildlife Conservation, Inc.

Meyer A. 1989. Cost of Morphological Specialization: Feeding Performance of the Two Morphs in the Trophically Polymorphic Cichlid Fish, *Cichlasoma citrinellum*. Oecologia 80:431–436.

Milton K. 1979. Factors Influencing Leaf Choice by Howler Monkeys: A Test of Some Hypotheses of Food Selection by Generalist Herbivores. American Naturalist 114:362–378.

Milton K. 1981. Estimates of reproductive parameters for free-ranging *Ateles geoffroyi*. Primates 22:574-579.

Milton K. 1984. The role of food-processing factors in primate food choice. In: Rodman PS, Cant JGH, editors. Adaptations for Foraging in Nonhuman Primates. Columbia University Press. p 249–279.

Milton K. 2006. Analyzing nutritional ecology. In: Hohmann G, Robbins M, Boesch C, editors. Feeding Ecology in Apes and Other Primates: Ecological, Physiological and Behavioural Aspects. New York: Cambridge University Press. p 381–396.

Nakagawa N. 2000. Seasonal, sex, and interspecific differences in activity time budgets and diets of patas monkeys *(Erythrocebus patas)* and tantalus monkeys *(Cercopithecus aethiops tantalus)*, living sympatrically in northern Cameroon. Primates 41:161–174.

Norconk MA, and Kinzey WG. 1994. Challenge of neotropical frugivory: Travel patterns of spider monkeys and bearded sakis. Am. J. Primatol. 34:171–183.

Oates JF. 1987. Food distribution and foraging behavior. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate Societies. Chicago: University of Chicago Press.

Parsons PE, and Taylor CR. 1977. Energetics of brachiation versus walking: a comparison of a suspended and an inverted pendulum mechanism. Physiological zoology 50:182–188.

Perret M, Chautems A, Spichiger R, Peixoto M, and Savolainen V. 2001. Nectar Sugar Composition in Relation to Pollination Syndromes in Sinningieae (Gesneriaceae). Annals of Botany 87:267–273.

Riba-Hernandez P, and Stoner K. 2005. Massive destruction of Symphonia globulifera (Clusiaceae) flowers by Central American spider monkeys *(Ateles geoffroyi)*. Biotropica 37:274–278.

Riedel J, Franz M, and Boesch C. 2010. How feeding competition determines female chimpanzee gregariousness and ranging in the Taï National Park, Côte d'Ivoire. Am. J. Primatol. 73:305–313.

Riopelle AJ, Hill CW, Li S-C, Wolf RH, Seibold HR, and Smith JL. 1974. Protein deprivation in primates. I. Nonpregnant adult rhesus monkeys. The American Journal of Clinical Nutrition 27:13–21.

Riopelle AJ, Hill CW, Li SC, Wolf RH, Seibold HR, and Smith JL. 1975. Protein deficiency in primates. IV. Pregnant rhesus monkey. The American Journal of Clinical Nutrition 28:20–28.

Robinson BW, and Wilson DS. 1998. Optimal Foraging, Specialization, and a Solution to Liem's Paradox. The American Naturalist 151:223–235.

Rosenberger A, Halenar L, Cooke S, and Hartwig W. 2008. Morphology and evolution of the spider monkey, genus Ateles. In: Campbell C, editor. Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles. 1st ed. Cambridge University Press. p 19–50.

Rosenberger AL. 1992. Evolution of feeding niches in new world monkeys. Am. J. Phys. Anthropol. 88:525–562.

Rothman JM, Chapman CA, and Pell AN. 2008a. Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. Am. J. Primatol. 70:690–694.

Rothman JM, Dierenfeld ES, Hintz HF, and Pell AN. 2008b. Nutritional quality of gorilla diets: consequences of age, sex, and season. Oecologia.

Ruby J. 2000. Chemical Composition of Fruits and Leaves Eaten by Short-Nosed Fruit Bat, *Cynopterus sphinx*. Journal of Chemical Ecology 26:2825–2841.

Schaefer HM, Schmidt V, and Wesenberg Jens. 2002. Vertical Stratification and Caloric Content of the Standing Fruit Crop in a Tropical Lowland Forest. Biotropica 34: 244-253.

Schoener TW. 1971. Theory of Feeding Strategies. Annual review of ecology and systematics 2:369–404.

Simmen B, Bayart F, Marez A, and Hladik A. 2007. Diet, Nutritional Ecology, and Birth Season of *Eulemur macaco* in an Anthropogenic Forest in Madagascar. Int J Primatol 28:1253–1266.

Smith J, Grant PR, Grant BR, Abbott IJ, and Abbott LK. 1978. Seasonal variation in feeding

habits of Darwin's ground finches. Ecology 59:1137–1150.

Steenbeek R, and van Schaik CP. 2001. Competition and group size in Thomas's langurs *(Presbytis thomasi)*: the folivore paradox revisited. Behav Ecol Sociobiol 49:100–110.

Sterck EHM, Watts DP, and van Schaik CP. 1997. The Evolution of Female Social Relationships in Nonhuman Primates. Behav Ecol Sociobiol 41:291–309.

Strier KB. 1992. Atelinae adaptations: Behavioral strategies and ecological constraints. Am. J. Phys. Anthropol. 88:515–524.

Suarez S. 2006. Diet and Travel Costs for Spider Monkeys in a Nonseasonal, Hyperdiverse Environment. Int J Primatol 27:411–436.

Symington M. 1990. Fission-fusion social organization in Ateles and Pan. Int J Primatol 11:47–61.

Takahashi T, and Koblmüller S. 2011. The Adaptive Radiation of Cichlid Fish in Lake Tanganyika: A Morphological Perspective. International Journal of Evolutionary Biology 2011:1–14.

Ungar P. 2004. Dental topography and diets of *Australopithecus afarensis* and early Homo. Journal of Human Evolution 46:605–622.

Vogel ER, Crowley BE, Knott CD, Blakely MD, Larsen MD, and Dominy NJ. 2011. A Noninvasive Method for Estimating Nitrogen Balance in Free-Ranging Primates. Int J Primatol.

Vogel ER, Haag L, and Setia TM. 2009. Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. Am. J. Phys. Anthropol. 140:716–726.

Wallace RB. 2005. Seasonal Variations in Diet and Foraging Behavior of *Ateles chamek* in a Southern Amazonian Tropical Forest. Int J Primatol 26:1053–1075.

White T. 1993. The inadequate environment: nitrogen and the abundance of animals. 1st ed. Berlin: Springer-Verlag.

Wolff D. 2006. Nectar Sugar Composition and Volumes of 47 Species of Gentianales from a Southern Ecuadorian Montane Forest. Annals of Botany 97:767–777.

Wrangham R. 1979. On the evolution of Ape Social Systems. Social Science Information 18:336–368.

Wrangham R. 1980. An Ecological Model of Female-Bonded Primate Groups. Behaviour 75:262–300.

Yamashita N. 1998. Functional dental correlates of food properties in five Malagasy lemur

species. Am. J. Phys. Anthropol. 106:169–188.

Yamashita N. 2008. Chemical Properties of the Diets of Two Lemur Species in Southwestern Madagascar. Int J Primatol 29:339–364.

Yeager CP. 1989. Feeding ecology of the proboscis monkey *(Nasalis larvatus)*. Int J Primatol 10:497–530.

Appendix A

Composition of Runaway Creek Nature Reserve phenology trail at the end of the study period (October 2010).

Family	Genus	Species	Number on Trail
Anacardiaceae	*Metopium*	*brownei*	5
Anacardiaceae	*Spondias*	*mombin*	5
Anacardiaceae	*Astroneum*	*graveolens*	5
Apocynaceae	*Stemmadenia*	*donnell-smithii*	5
Apocynaceae	*Aspidosperma*	*megalocarpon*	6
Arecaceae	*Sabal*	*mmauritiiformis*	2
Arecaceae	*Attalea*	*cohune*	5
Arecaceae	*Sabal*	*yapa*	3
Boraginaceae	*Cordia*	*diversifolia*	5
Burseraceae	*Protium*	*copal*	5
Burseraceae	*Bursera*	*simaruba*	5
Caesalpinaceae	*Dialium*	*guianense*	5
Cecropiaceae	*Cecropia*	*peltata*	5
Combretaceae	*Terminalia*	*amazonia*	5
Ebeneceae	*Diospyros*	*bumelioides*	5
Euphorbiaceae	*Ampelocera*	*hottlei*	2
Euphorbiaceae	*Drypetes*	*browneii*	7
Fabaceae	*Schizolobium*	*parahyba*	2
Fabaceae	*Caesalpinia*	*gaumeri*	5
Lauraceae	*Nectandra*	*belizensis*	4
Meliaceae	*Guarea*	*grandifolia*	3
Mimosaceae	*Acacia*	*cookii*	6
Moraceae	*Ficus*	sp.	15
Moraceae	*Trophis*	*racemosa*	5
Moraceae	*Castilla*	*elastica*	5
Moraceae	*Brosimum*	*alicastrum*	6
Moraceae	*Pseudolmedia*	*spuria*	5
Palmae	*Cryosophila*	*stauracantha*	5
Rubiaceae	*Guettarda*	*combsii*	6
Sapindaceae	*Cupania*	*belizensis*	5
Sapotaceae	*Pouteria*	*amygdalina*	5
Sapotaecae	*Manilkara*	*chicle*	5
Simaroubaceae	*Simarouba*	*glauca*	5
Tiliaceae	*Luhea*	*speciosa*	5
TOTAL			172

Appendix B
Runaway Creek Nature Reserve Spider Monkey Ethogram
(Kayla Hartwell 2011)

SOLITARY BEHAVIOUR		
F	Feed/ Forage	Focal eats or actively searches for food items (also includes smelling fruits). Indicate plant species and plant part consumed.
DK	Drink	Focal consumes water. Indicate where (tree hole, palm, etc.) and how (i.e. dunks hand in water source and drips water into mouth off of knuckles, fingers, wrists or sucks water off fingers, collects water in palm of hand and brings to mouth, brings head to water source and drinks directly).
I	Inactive	Focal sits, lies down or hangs (eyes can be open or closed).
T	Travel	Focal moves (does not include moving around in a tree while foraging for food).
AUG	Auto groom	Focal grooms itself (does not include scratching).
NSP	Non-social play	Solitary play, i.e. swinging from tail, playing with broken branch
PLS	Place sniff/lick	Focal touches nose or tongue to branch/substrate. Usually performed by males directly after a female got up from sitting on a branch/substrate (if known, indicate who was sitting there prior to place sniff). Also indicate if place sniffing/licking urine (rare behaviour).
CR	Chest rub	Focal rubs chest back and forth against substrate/branch (rare behaviour).
GR	Genital rub	Focal sits and rubs ano-genital region back and forth along branch (rare behaviour).
VG	Vigilance	More alert then just scanning an area, usually in response to potential danger, i.e. large raptor flies over (rare behaviour).
SOCIAL BEHAVIOUR (indicate d and r)		
d	Direct	Focal animal initiates action.
r	Receive	Another animal initiates action to focal animal.
SN	Sit Near	Focal is within 2 meters (2 arms reach) of other individual(s). Record ID or age/sex class of other individual(s).
SC	Sit Close	Focal is within 1 meter (but not in contact) with other individual(s). Record ID or age/sex class of other individual(s).

SIB	Sit in Body Contact	Focal is in physical contact with other individual(s). Record ID or age/sex class of other individual(s).
a	Approach	Focal directs (or receives) an approach within 2 meters of other individual. Record ID or age/sex class of other individual(s) involved and director/receiver.
l	Leave	Focal directs (or receives) a leave, i.e. one individual distances itself from another individual. Record ID or age/sex class of other individual(s) involved and director/receiver.
pb	Pass By	Focal directs (or receives) a pass by, i.e. one individual passes within 2 meters of another and keeps on moving without stopping. Record ID or age/sex class of other individual(s) involved and director/receiver.
ALG	Allogroom	Focal directs (or receives) allogroom from other individual (5 sec break between bouts). Record ID or age/sex class of other individual involved and director/receiver.
SG	Solicit Groom	Focal directs (or receives) solicitation to allogroom, i.e. one individual presents body part (usually lifts arm up to present armpit area) to another individual for grooming. Record ID or age/sex class of other individual involved and director/receiver.
SP	Social Play	Focal plays with other individual (chasing, wrestling, mock biting and usually accompanied by play vocalizations). Record ID or age/sex class of other individual(s) involved.
NU	Nurse	Focal nurses their offspring.
PSE	Pectoral Sniff and Embrace	Focal wraps one or two arms around another's shoulder, head, or waist and places its nose near to the other's pectoral gland (around the neck/chest or arm pit region). Usually accompanied by a guttural whinny-like vocalization. Can vary in intensity and last up to several seconds. Pectoral sniff and embrace can also occur independently from one another. Record ID or age/sex class of other individual involved and director/receiver.
WC	Wound Clean	Focal directs (or receives) cleaning of wound by touching and licking. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
GRP	Grapple	Focal engages in sustained contact (usually lasting several minutes up to over an hour) with another individual and behaviour may contain, but is not limited to: facial greeting/touching, embracing, tail wrapping, pectoral sniffing, and genital contact. Animals may also move apart, maintaining intense face to face visual contact then move together. Usually accompanied with high pitch whistles, pants, and soft growl vocalizations. Usually observed between subadult and adult males or occasionally subadult males and adult females. Record ID or age/sex class of individuals involved, and director/receiver if obvious (rare

		behaviour).
ALC	Allocarry	An individual (other than mother) carries an infant/juvenile while traveling. Record ID or age/sex class of individuals involved (rare behaviour).
IH	Infant Handle	An individual (other than mother) sits and handles an infant, letting infant climb on and/or cling to them. Record ID or age/sex class of individuals involved (rare behaviour).
SIH	Solicit Infant Handle	Individual (other than mother) presents chest/stomach area to infant for it to climb on (rare behaviour).
CP	Copulation	Self-explanatory. Record ID or age/sex class of individuals involved (rare behaviour).
KF	Kissy-Face	Focal gazes in direction of other and purses lips outward in a wide kiss-like gesture, usually accompanied with a guttural whinny vocalization. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
GT	Genital Touch	Focal (directs or receives) touches/sniffs/licks the anogenital region of another individual. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
FS	Finger sniff	Focal (directs or receives) touches genitals of another individual and sniffs their fingers. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
SCO	Solicit copulation	Focal directs or receives invite to copulate (copulation may or may not follow) (rare behaviour). Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
OS	Out of Site	Focal is out of view.
	AGGRESSION	
AGG	Aggression	Record ID or age/sex class of other individual(s) involved and director/receiver. Indicate if aggression was in the form of a coalition and describe intensity: 1=lunge, open mouth threat, vocalizations (growling, screams), short in duration 2= same as above, but continued chase with no physical contact 3= same as above with physical contact (slaps, hits, grabs, bites) but no serious injury 4= same as above with noticeable injury (wounds, bleeding, limping)
TD	Threat display	Focal threatens observer, potential predator (or nothing obvious) by growling and/or shaking/breaking branches.

PBT	Piggy Back Threat	2+ individuals pile on top of each other in a threat display
DP	Displacement	Individual displaces another. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
AV	Avoid	Individual moves out of the way when another individual approaches. Record ID or age/sex class of other individual involved and director/receiver.
VOCALIZATIONS		
WHV	Whinny	most common vocalization, wavelike frequency modulation that varies in length tone and harshness
THV	Tee-Hee	similar sound to a whinny but a shorter 2 note call
OBV	Ook-Bark	Alarm call, harsh short notes varying in intensity.
SCV	Scream	given when individual is under attack or physical threat
GRV	Growl	Harsh noisy sound vocalized during threat display or aggression and rough physical contact play.
LCV	Long Call	Very loud and long call given in an attempt to re-establish contact with other sub-groups.
PLV	Play Vocalizations	Light or heavy panting and growling used during social play. Can vary in intensity
CHV	Chirps	High pitch short notes given repeatedly, usually during threat display or aggression.
TSV	Tschook	Similar to a long call but less intense, harsh gurgle in the throat.
HPWV	High-Pitch Whistle	a flat high pitch vocalization held for 2-3 seconds and usually repeated – kind of like a whine

Appendix C
Full GLM Output

Effect		F	df	Significance
Flowers		-	-	-
	Feed	3.269	13	**0.009**
	Social	1.302	13	0.289
	Travel	5.381	13	**0**
Sex				
	Feed	0.01	1	0.921
	Social	0.441	1	0.514
	Travel	0.252	1	0.621
Age				
	Feed	1.142	1	0.298
	Social	4.836	1	**0.04**
	Travel	0.089	1	0.769
*Flowers*Sex*				
	Feed	0.201	12	0.997
	Social	0.256	12	0.991
	Travel	2.089	12	0.07
*Flowers*Age*				
	Feed	0.199	12	0.997
	Social	0.277	12	0.987
	Travel	0.88	12	0.579
*Sex*Age*				
	Feed	1.991	1	0.174
	Social	0	1	0.984
	Travel	14.147	1	**0.001**
*Flowers*Sex*Age*				
	Feed	0.194	8	0.989
	Social	0.41	8	0.901
	Travel	1.801	8	0.136