The Nutritional Ecology of Spider Monkeys (*Ateles chamek*) in the Context of Reduced-Impact Logging

Peruvian spider monkey (*Ateles chamek*) in the forestry concession La Chonta Photo by Helga Peters

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"The land is one great wild, untidy, luxuriant hothouse, made by Nature for herself."

Charles Darwin, 1845. The Voyage of the Beagle.

DECLARATION

This thesis is my own work except where otherwise acknowledged (see Acknowledgements and Preface).

Annika M. Felton
February 2008.

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PREFACE

With the exception of Chapter 1 (Introduction) and Chapter 6 (Conclusion), this thesis consists of a series of interrelated manuscripts. These manuscripts are either accepted for publication or submitted for publication. Each manuscript is presented as it appears, or will appear, in the relevant journal with the exception of minor changes in style and formatting. I cross-reference between these manuscripts using their respective chapter numbers. The vast majority of the work that contributed to this thesis was carried out by the primary author (Annika Felton), including literature searches, project design, data collection, laboratory analyses, data analysis, and manuscript write-up. However, co-authors are included on each manuscript, acknowledging their contributions to each particular aspect of the research. David Lindenmayer contributed to the overall experimental design, provided guidance regarding the organization of the research, made important contributions to each paper, and proof-read all manuscripts. Adam Felton contributed in terms of formulating ideas, project design, logistical support, data collection, and proof reading through all stages of the project. Jeff Wood was involved in chapters 2, 3 and 4. He provided statistical advice regarding the appropriate data analysis to use and the interpretation of results. Bill Foley was involved in chapters 3, 4 and 5. He contributed with initial design of the aspects of the project that concerned food collection and preparation, provided guidance of the laboratory work and the subsequent interpretation of nutritional data. Ian Wallis, who was involved in chapters 3 and 4, also guided chemical analyses and interpretation of the data, in particular the *in vitro* digestibility assay. David Raubenheimer (chapters 3 and 4) and Stephen Simpson (Chapter 3) guided the geometric analysis and interpretation. Because the primary chapters of this thesis are manuscripts developed for independent publication in scientific journals, some repetition between chapters was unavoidable.

SUMMARY

Selective harvesting of timber in tropical forests can remove substantial amounts of primate food sources, resulting in significant reductions in population densities. As frugivorous primates are important seed dispersers in tropical forests, it is crucial for long-term ecological sustainability to maintain their populations within forestry concessions. One way of achieving this goal is to gather relevant information regarding the importance of commercial timber tree species in the diet of seed dispersing primates and ultimately suggest adjustments to timber extraction rates to minimize detrimental impacts on primate food resources.

In this thesis I first describe the diet and temporal patterns of food consumption by the Peruvian spider monkey, *Ateles chamek*, inhabiting a semi-deciduous moist forest that is incorporated in a certified forestry concession in lowland Bolivia (Chapter 2). I then determine what governs their diet selection (Chapter 3), and analyse how this nutritional strategy influences seasonal diets and the resultant nutritional states of individuals, and estimate the relative value of different food sources (Chapter 4). These threads of information are combined to assess the importance of timber tree species in the diet of these primates as a basis for recommendations for forest management and primate conservation (Chapter 5). As such, an overreaching aim of this thesis is to contribute to the understanding of the effects of certified tropical forestry on biodiversity conservation.

I conducted empirical investigations within Bolivia, in the lowland forest of the Guarayos Forest Reserve, Departmento Santa Cruz. Research was conducted within an unharvested section of the 100,000 hectare forestry concession “La Chonta”, from September 2003 to September 2004. During habituation of the spider monkeys I, with the help of assistants, established a network of trails in the study community’s territory (for definition on “spider monkey community”, see 1.3), which covered an area of 360-400 ha. We used this trail network for daily follows, monthly phenology surveys, and vegetation surveys. Following habituation, I systematically collected detailed behavioural data on the spider monkeys from February 2004 to September 2004. As part of these daily follows I conducted continuous observations of the same focal animal (FA) from dawn to dusk, paying special attention to feeding. Eight

of these FAs were adult males and ten were adult females. My team also collected and dried samples of the food consumed. These samples were later analysed in a laboratory at The Australian National University to estimate their nutritional content.

In this thesis I first assess dietary composition and feeding time budgets in relation to temporal variation in abundance, duration, and synchrony of different food items in the territory of this community of spider monkeys (Chapter 2). Throughout the period of detailed feeding data collection, the spider monkeys used *Ficus* as a staple food resource, in particular figs of the commercial timber tree species *Ficus boliviana*[1]. Figs comprised 45% of total feeding time and were consumed extensively even during times of high overall food availability. This is contrary to the general expectation that for Neotropical frugivores, *Ficus* is a fall-back food in times of fruit scarcity, rather than a staple food resource (for definitions of these terms see 1.4). Surprisingly, the spider monkeys spent 18% of their feeding time eating unripe figs. This is despite these primates being considered "ripe fruit specialists". The spider monkeys consumed unripe figs throughout the year, including periods when ripe figs and other ripe fruit were abundant. We also identify important fall-back foods for the spider monkeys in this forest, in particular the ripe fruit of *Myrciaria* (sahuinto).

In Chapter 3 I move away from conventional analytical methods used in nutritional ecology, and analyse my detailed data-set on daily nutrient intake by applying a multidimensional geometric framework. This novel way of analysing primate nutrition allowed me to understand what governs the diet selection of the spider monkeys. In Chapter 3 I show that nutrient balancing is the primary goal of food intake in a non-human primate. The analysis shows that alternative hypotheses traditionally used to explain vertebrate diet selection, such as energy or protein maximization, or avoidance of plant secondary metabolites, cannot explain the observed pattern of nutrient intake. Instead I show that protein intake by spider monkeys mimicked that of humans: protein was regulated more tightly than carbohydrates or fats, and disproportionately influenced total energy intake. The monkeys' daily intake of available protein was maintained at a mean of 11 g (equating to 0.19 MJ ± 0.01 SE), whereas non-protein energy varied between 0.7-6.2 MJ (mean 1.82 MJ ± 0.82 SE). These findings have far-ranging implications. For

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[1]. The taxonomy of this species is uncertain at the time of printing. This species may be *Ficus insipida* (synonym *F. glabrata*), but because the name *F. boliviana* is the accepted classification employed by Bolivian researchers I have chosen to use it throughout the thesis. Please contact the author for updated nomenclature.

example, the distinct similarity between the nutritional underpinnings of *Homo* and *Ateles* diet selection indicates that the origin of human susceptibility to obesity may date before the previously speculated Paleolithic era. Furthermore, this similarity suggests that an adjustment of the macro-nutritional balance of diets as a means to manage human obesity might similarly be an option for mitigating the common problem of obesity in captive primates. The results also provide a deep understanding of primate nutritional ecology that is directly applicable to forest management and primate conservation. For instance, figs of the commercial timber species *Ficus boliviana* appear to be a nutritionally-balanced food for spider monkeys. Nutritionally-balanced food sources that are used extensively by a wild population may need special attention in conservation planning, e.g. as the basis for excluding certain tree species from logging, or as target tree species for establishment in vegetation restoration.

In Chapter 4 I assess the influence of protein-dominated macro-nutrient balancing on daily and seasonal nutritional intakes, estimate the nutritional value of different foods and interpret unusual food choices. By analysing nutritional data under the Geometric Framework, I found that individuals would reach their daily end point in nutritional space (balance between protein and non-protein energy intake) by using one of three strategies: consuming nutritionally-balanced foods; alternating between nutritionally complementary foods; or ingesting large amounts of energy-dense fruit and thereby consuming “surplus” energy (more than needed for maintenance of body weight, Knott 1998). The strategy employed and the resultant nutritional state of individuals depended upon the seasonal availability of different types of food. For example, the food available during the late peak fruiting season provided them with 50% more non-structural carbohydrates (TNC) and lipids than the fall-back diet during the period of ripe fruit scarcity. The analysis also reveals that figs were a readily available, nutritionally-balanced, and mineral-rich food resource. This allowed spider monkeys at times to concentrate their feeding to a few trees and thus most likely reduce energetic costs and predation risk. The data also indicate that the reason why this community consumed unusually large amounts of unripe figs was because unripe figs constituted an easily harvestable, nutritionally rewarding, and continuously available complementary food. In fact, contrary to the common perception of figs as not being a preferred food by tropical frugivores when other options are available, my results indicate that the consumption of a diverse array of different fruit was used by our study animals as a strategy for getting through periods of fig scarcity rather than the other way around.

The knowledge gained in chapters 2 - 4 was combined to make an assessment of the importance of commercial timber tree species (TTS) in the diet and nutritional ecology of this community of spider monkeys (Chapter 5). My study community inhabits a forestry concession where reduced-impact logging practices are applied. Reduced-impact logging (RIL) was developed, in part, to minimize the negative impacts of logging on biodiversity and incorporates a variety of techniques aimed at lowering levels of harvesting damage to the residual stand. Despite these measures, logged areas in La Chonta have been found to sustain only 25% of the spider monkey population density found in unlogged areas. My assessment revealed that spider monkeys occupying unlogged sections of this forest spent 47% of their feeding time eating items from TTS which equated with approximately 50% of their total intake macro-nutrients. Timber tree species comprised their staple food, dominated their peak season diet, and also played a significant part of their fall-back diet. Because spider monkeys exhibited a distinct preference for foraging within individuals of TTS which were large enough to be harvested, I estimated that under current timber extraction intensities spider monkeys lose significant proportions of their food sources. I suggest that for territorial non-volant animals like spider monkeys, the most efficient means by which their populations can be secured, and thereby their ecological services maintained, would be to place harvesting limits on TTS that function as important food sources. My results indicate that such limits should be considered for the timber tree species *Ficus boliviana, Spondias mombin* and *Pouteria nemorosa*.

Six general conclusions arise from this thesis:

1. Feeding ecology of *Ateles chamek* in La Chonta differed from other documented spider monkey diets because of the dietary dominance of ripe and unripe figs.
2. Diet selection was governed by protein-dominated macro-nutrient balancing, rather than energy or protein maximization, or avoidance of plant secondary metabolites.
3. The food intake strategy employed by individuals and their resultant nutritional state depended upon the seasonal availability of different foods.

Due to seasonal availability of fruits rich in soluble carbohydrates and lipids, intake of these macro-nutrients was 50% higher during peak fruiting season than during the period of fruit scarcity.

4. Figs were nutritionally-balanced foods for spider monkeys, and the inclusion of a diverse array of ripe fruits in their diet appeared to be used as a strategy for persisting through times of fig scarcity.
5. Timber tree species provided spider monkeys with 50% of their macro-nutrient intake, comprised their staple food, and dominated their peak season and fall-back diets.
6. Under current prescriptions for timber extraction the spider monkeys in La Chonta are expected to lose significant proportions of their food sources. This is a likely explanation for the observed declines in population density post-logging. Harvesting limitations should be considered for the timber tree species *Ficus boliviana, Spondias mombin* and *Pouteria nemorosa*.

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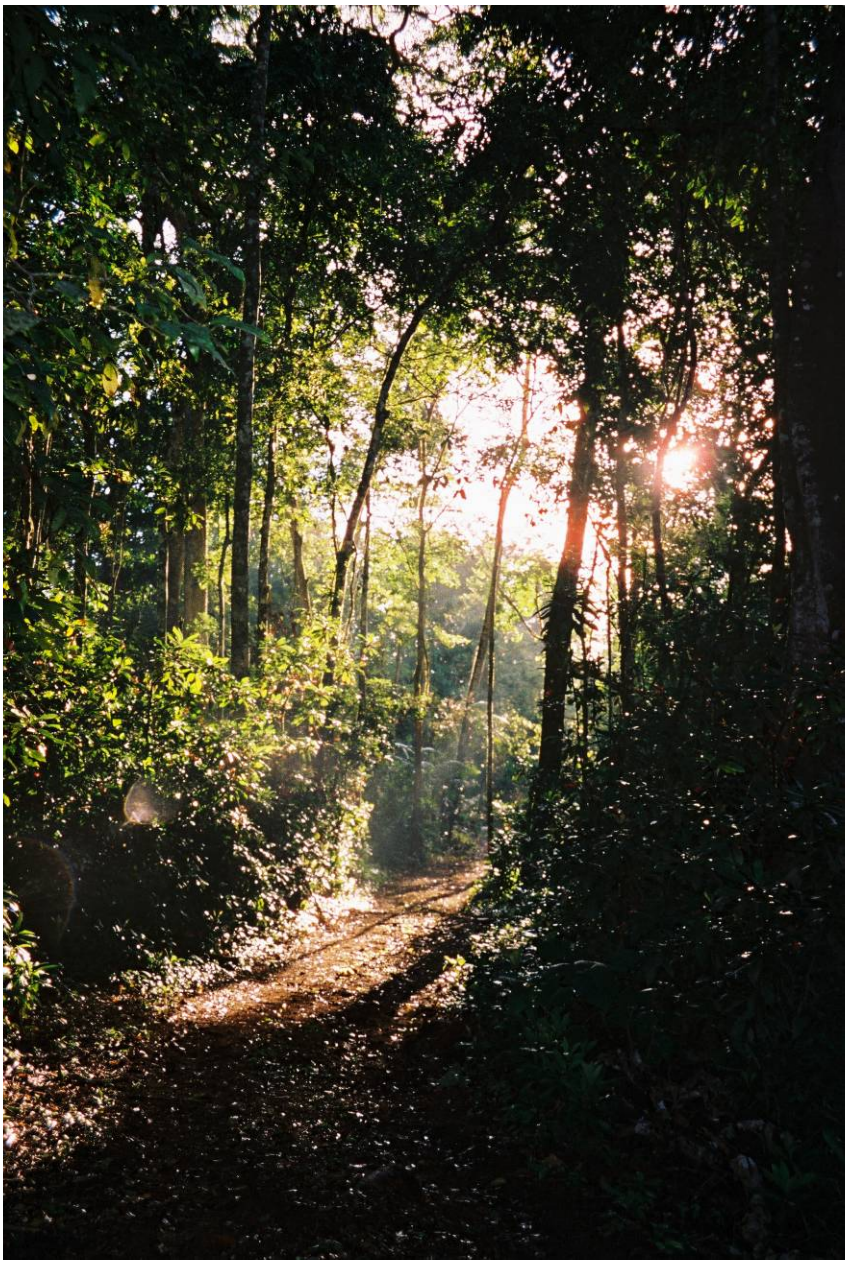

Photo by Petter König

On approach to our research camp in the La Chonta forestry concession.

Chapter 1 – Introduction

1.1. Background to this project

Primates comprise between 25% and 40% of the frugivore biomass in tropical forests (Chapman 1995) and are responsible for the dispersal of a large proportion of the seeds removed from parent trees (Chapman & Onderdonk 1998). While trees provide the majority of food for frugivous primates, the primates in turn often enable the seeds of consumed fruits to be effectively dispersed, significantly increasing their likelihood of germination (Howe 1984; Wrangham, Chapman & Chapman 1994; Chapman 1995; Chapman & Chapman 1996). For these reasons, reductions in the densities of frugivorous primates may have deleterious effects on forest recovery and regeneration (Chapman & Chapman 1996; Chapman & Onderdonk 1998).

Spider monkeys (see section 1.3) play an important role in seed dispersal in Neotropical forests (Chapman & Russo 2007). Their foraging behaviour results in relatively high survivorship of the seeds they disperse, as they ingest large quantities of whole seeds of varying sizes and often deposite them far away from the parent plant with a widely scattered spread on the ground. In some forests, spider monkeys are the sole primate dispersers for tree species that produce very large seeds (Dew 2001). Some of the ecological characteristics that make spider monkeys especially good seed dispersers - arboreal, large-bodied, and highly frugivorous – in combination with their slow reproductive rate, leads to a high sensitivity to habitat disturbance (Skorupa 1986; Johns & Skorupa 1987; Peres 1994b; Sorensen & Fedigan 2000; Felton et al. 2003). As a result of increasing pressures from human populations, some spider monkey species have declined in range and density and are classified as threatened or vulnerable to extinction (Conservation-International 2005).

There have been no detailed studies of the effects of logging on primates in the Neotropics (Plumptre & Grieser Johns 2001). However, recent surveys conducted in the certified forestry concession of La Chonta in Bolivia, have shown that areas which had been logged one and two years previously supported only 25% of population densities found in comparable unlogged sections of the forest (Fredericksen et al. 2007). Similarly, population densities of other important seed dispersing vertebrate taxa, such as howler monkeys, guans (Fredericksen et al. 2007) and toucans (Felton *et al.* 2008a) also exhibited reduced population densities within logged areas of this concession. The significant difference in spider monkey density between logged and unlogged areas (Fredericksen et al. 2007) occurred despite the fact that reduced-impact logging (RIL) techniques had been employed in this forestry concession.

Reduced-impact logging is a modified form of selective logging that incorporates a variety of techniques aimed at lowering levels of damage to the residual stand. The implicit assumption is that these actions, in combination with strict hunting bans, will reduce logging related impacts on biodiversity (Heinrich 1995; Uhl *et al.* 1997; Putz, Sirot & Pinard 2001). Research suggests that RIL does cause less damage to forest structure compared to conventional selective logging techniques used in tropical forests (Pereira *et al.* 2002; Asner *et al.* 2004; Huth, Drechsler & Kohler 2004). However, RIL is still a form of commercial forestry that increases the frequency and extent of canopy discontinuities (Jackson, Fredericksen & Malcolm 2002). The capacity of RIL concessions to retain their original complement of biodiversity is not well known (Bojanic & Bulte 2002; Dauber, Fredericksen & Peña 2005) and whether current RIL is an effective means towards sustainable forestry is debated (Dauber *et al.* 2005; Keller *et al.* 2007; Felton *et al.* 2008a). It is of ever increasing importance that natural forest management in the Neotropics is firmly based on science, as the overriding aim is to ensure sustainability of both timber resource extraction and biodiversity maintenance (Guariguata & Pinard 1998).

Under current logging regimes in Bolivia, timber is not being extracted at a sustainable rate (Dauber et al. 2005). Like most forestry concessions in the tropics, Bolivian forestry concessions depend on natural regeneration rather than planting (Mason & Putz 2001). Unfortunately, the Bolivian forestry industry is plagued by the inadequate regeneration of their most important timber species (Mostacedo & Fredericksen 1999). The documented low rates of seedling and sapling establishment may result from present and past logging activities. First, reduced regeneration may be caused by damage to timber trees in advanced stages of regeneration caused during timber extraction (Felton et al. 2006). Second, the number of seed trees may be deficient due to past high-grading practices (Mostacedo & Fredericksen 1999). Finally, there is evidence to suggest that current silvicultural treatments being promoted are not sufficient to ensure natural regeneration in the timber tree species of concern (Fredericksen & Putz 2003; Peña-Claros *et al.* 2007; but see Sist & Brown 2004). Notably, all of these problems are likely to be compounded in the long term by reductions in the population densities of primate seed dispersers.

To maintain populations of important seed dispersers, such as frugivorous primates, forest managers may need to place harvesting limits on those timber tree species that play critical roles in the ecology of these animals. However, to formulate such directives, detailed, quantitative information is needed regarding *which* timber species are of high concern and *to what extent* primates depend on these tree species for their nutrition. The gathering of such information poses considerable practical challenges, especially in studies of arboreal free-ranging monkeys. This is because it requires detailed data on feeding behaviour from individual animals over continuous periods, relevant analyses of all foods consumed, and an analytical framework for dealing with the complex, multivariate nature of nutritional data.

This study was designed to gather the relevant data needed to determine the extent to which timber tree species are important in the ecology of the Peruvian spider monkey (*Ateles chamek*), and whether their dependence on timber tree species can explain why spider monkey densities are so much lower in logged than unlogged parts of the La Chonta concession. In most studies, primate diets are expressed as time spent foraging and feeding. This is despite the fact that the volume of food, and associated nutrients, ingested by individuals can vary significantly depending on the type and size of food, age/sex of individuals, and the abundance of the food (Milton 1984; Oftedal 1991). Instead of relying solely on feeding time assessments of the contribution of timber tree species to the spider monkeys, I conducted a detailed quantification of the nutrients which spider monkeys obtained from each plant species. I also evaluated the food sources' relative importance using a nutritional ecology approach. I expand upon these aims below.

1.2. Primate nutritional ecology

Feeding is a fundamental interaction between an animal and its environment. Nutrition is thus closely related to many aspects of wildlife ecology, including for example population dynamics, mating systems, habitat use, and predator-prey interactions (Ortman et al. 2006). Nutritional ecology can be defined as the field of investigation into the means by which animals procure macro- and micro-nutrients from their habitat (Lambert 2007). Primates, like all other animals, must make choices regarding what to include in their daily diet - choices that will in turn influence their nutritional state, and ultimately their health and fitness (Altmann 1998; Beehner et al. 2006). Primates are faced with many challenges when trying to meet their nutritional needs. These challenges span several spatial and temporal scales, from the nutritional, chemical, or structural qualities of food items (Milton 1993a; Lambert 2007), to the habitat-wide availability of different foods (van Schaik, Terborgh & Wright 1993; Stevenson, Quinones & Ahumada 2000).

Regardless of whether a primate predominantly feeds on fruit, leaves or animal matter, individuals require the full suite of nutrients required by most mammals (protein, carbohydrates, lipids, vitamins and minerals, Oftedal 1991). It has long been a focus of nutritional ecologists to understand the primary nutritional drivers behind food choice in primates and other animals. The insights gained through nutritional ecology are relevant for conservationists as they enable us to understand food choices made by wildlife (Robbins et al. 2007), and determine which critical nutritional resources are missing from the diet of animals whose habitat has been disturbed by humans (Raubenheimer & Simpson 2006).

There are four major schools of thought in nutritional ecology, each of which proposes that diet selection subserves a different primary nutritional goal:

(i) energy maximization (Schoener 1971);

(ii) nitrogen maximization (Mattson 1980; White 1993);

avoidance of plant secondary metabolites (Freeland & Janzen 1974; Dearing, Foley & McLean 2005)

(iii) nutrient balancing (Raubenheimer & Simpson 2004; Robbins et al. 2007).

It is not easy to quantify the relative influence of these different nutritional goals, especially in studies of wild arboreal animals, such as spider monkeys, that travel quickly and over large distances in the canopies of tropical forests.

The field of primate nutritional ecology has predominantly interpreted patterns of nutrient intake by assessing and presenting data in the forms of tables. The field has not as yet embraced recent approaches to nutritional theory which use multidimensional assessments of macro-nutrients, such as geometric analyses (Raubenheimer & Simpson 2004). The main advantage with geometric analyses is that they enable a clear understanding of the trade-offs made by animals while regulating their nutritional balance (Raubenheimer & Simpson 2004). The geometric framework (GF) was designed to assess the relative priorities assigned by animals to different food components, e.g. the relative importance of different macro-nutrients when animals make food choices (Simpson & Raubenheimer 1993). The information gleaned from geometric analyses is likely to provide important implications not only for the field of primate nutritional ecology, but also for forest management, primate conservation and evolutionary theory.

1.3. Spider monkey ecology

Spider monkeys (genus *Ateles*, subfamily Atelinae) are found in varying forest types from Amazonian ever-green rainforest to deciduous forests throughout Central and South America (Kinzey 1997). There are 7 species of spider monkeys, one of which inhabit the lowland forests of Bolivia (*Ateles chamek* Humboldt 1812, Groves 2001). Spider monkeys generally prefer primary tall forest but have also been observed to use regenerating secondary forests with a canopy as low as 5 m (Green 1978; Chapman, Chapman & Glander 1989). They rarely leave the canopy strata, but use it for foraging, resting, travelling and all social interactions. The social unit of the spider monkey society is called *community*, normally including 15 – 40 individuals (Campbell in press). All members of the community are rarely observed together as they split into subgroups according to a fission-fusion pattern of social structure (van Roosmalen 1985; Symington 1988c; Chapman 1990).

Spider monkeys are among the largest primates in the Neotropical forests, with both males and females weighing 7.5 – 9 kg (Peres 1994c; Smith & Jungers 1997). These primates are considered to be ripe fruit specialists because they spend 75-90% of their foraging time consuming ripe fruit (Klein & Klein 1977; van Roosmalen 1985; Chapman 1987;1988; Symington 1988a; Cant 1990; Castellanos 1995; Kinzey

1997; Dew 2001; Wallace 2005). They can also temporarily switch to young leaves, flowers or unripe fruit at times of ripe fruit scarcity (van Roosmalen 1985; Chapman 1987; Symington 1988c; Cant 1990; Milton 1993b; Wallace 2005).

Energy is often proposed to be the primary driver behind atelines' diet selection (Rosenberger & Strier 1989; Strier 1992; Di Fiore & Rodman 2001). This is because ateline primates are frequently observed to preferentially select and consume large volumes of fruit that are rich in lipids and soluble carbohydrates (Castellanos 1995; Dew 2005; Di Fiore, Link & Dew in press).

1.4. Terminology used when classifying important primate food sources

One way of assessing the relative importance of food plants to primates is to classify them, when appropriate, into the categories of preferred foods, fall-back foods, and/or staple foods. *Preferred foods* can be defined as those foods that are eaten more often than would be predicted based on their availability (i.e. "overselected", *sensu* Leighton 1993). There is also the expectation by some researchers that preferred foods yield high energy return per unit foraging time compared to other food items (Krebs & Stephens 1986). *Fall-back foods* on the other hand are defined as items "assumed to be of relatively poor nutritional quality and high abundance, eaten particularly during periods when preferred foods are scarce" (see review in Marshall & Wrangham 2007). *Staple foods* have been defined in primate ecology as foods which are fed upon all year-round independently of the availability of preferred foods, and which are adequate nutritionally to allow the animal to subsist on them (Knott 2005; Marshall & Wrangham 2007). Categorizing foods using these definitions has proven to be useful, as primate population density has been found to be strongly influenced by the abundance of both staple foods (Oates 1996; Rogers et al. 2004), and fall-back foods (Weins 1977; Terborgh 1983; Marshall & Leighton 2006).

In this thesis I also discuss the importance of certain *peak season foods*. Of the foods included in the peak season diet I am particularly interested in the plant species which provide a disproportionate amount of energy (in the form of soluble carbohydrates and lipids). Other ateline species (*Lagothrix lagotricha cana*: Peres 1994a; *Ateles chamek*: Wallace 2005) are known to accumulate fat during periods of peak fruit abundance. This is a logical strategy for animals experiencing regular fluctuations in food supply. Seasonal accumulation of fat reserves may be crucial for survival and reproduction in these primates (see also Stevenson 2005).

Another way of determining the relative importance of foods for primates is to use the concept of *keystone species,* or *keystone resources*. While fall-back foods are resources utilized by species, keystone resources applies to whole communities (Marshall & Wrangham 2007). My study is at the scale of one primate species. For that reason, and because the term is fraught with difficulties and un-testable assumptions (Power & Mills 1995; Power et al. 1996; Hurlbert 1997; Stevenson 2005), I refrain from using this terminology to any great extent in this thesis.

1.5. Objective and aims

1.3.1 Objective one

Descriptions of the diets of frugivorous primates have traditionally contrasted the relative importance of different food items by the time spent feeding on them. Although other methods that assess the nutritional or mineral content of the diet can be used to gain a deeper understanding of the ecology of a species, time-based assessments are an excellent means of comparing study populations in different forest types and the relative dominance of different food sources in their diet. This type of analysis also highlights the importance of various fall-back and staple foods (for definitions see 1.4) and how these may differ between different study populations.

The first objective for this thesis was:

- To describe the diet of a community of spider monkeys (*Ateles chamek* Humboldt 1812) inhabiting a semi-deciduous moist forest in lowland Bolivia.

Specifically, I aimed to describe seasonal changes in diet composition in terms of the proportion of time spent feeding and analyse this information in relation to the temporal variation in abundance, duration and synchrony of different food items in their territory.

To satisfy this first objective, I collected data in the lowland semi-deciduous moist forest of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. I conducted the research in the 100,000 hectare forestry concession La Chonta, owned and managed by Agroindustria Forestal La Chonta. My study spanned the period from September 2003 to September 2004. I first habituated a community of spider monkeys inhabiting an unlogged section of the forest, and then conducted continuous data collection on the activities of focal individuals from dawn to dusk, focusing especially on feeding. Every month I collected data on the habitat-wide phenology of potential food species. I combined this data with tree species density information gained from a territory-wide vegetation survey, to estimate the availability of spider monkey food on a monthly basis.

1.3.2 Objective two

Understanding the nutritional strategies of animals in the wild has important implications for functional ecology and conservation biology, and has long been a focus of nutritional ecologists (e.g. Schoener 1971). A deep understanding of nutritional strategies are more than of academic interest as it helps us evaluate different food sources (Robbins et al. 2007) and understand what may be a crucial lacking resource for a species in a habitat disturbed by humans (Raubenheimer & Simpson 2006). Energy is often proposed to be the primary driver behind atelines' diet selection (Rosenberger & Strier 1989; Strier 1992; Di Fiore & Rodman 2001), as they are frequently observed to preferentially select and consume large volumes of energy-dense fruit (fruits rich in soluble carbohydrates and lipids, Castellanos 1995; Dew 2005; Di Fiore et al. in press).

The second objective for this thesis was:

- To determine what nutritional strategy governs the diet selection of *Ateles chamek* in La Chonta.

Specifically, I aimed to examine whether, by analyzing detailed data on nutrient intake and food selection from a wild primate, I could quantify the relative influence of the four alternative nutritional goals listed above in section 1.2.

I satisfied this second objective by collecting samples of the foods consumed by the spider monkeys and analysing them for their nutritional and chemical composition. I combined this information with detailed data on food consumption from days when I succeeded in following the same focal animal from dawn to dusk and collecting uninterrupted data on its feeding behaviour. The latter was a considerable practical challenge, which had not been successfully accomplished previously in studies of wild spider monkeys. To reach the goal of discovering the spider monkeys' nutritional strategy, I used the Geometric Framework for nutrition, an analytical framework designed for dealing with the complex, multivariate nature of nutritional data (Raubenheimer & Simpson 2004).

1.3.3. Objective three

A primate’s nutritional strategy influences not only which foods it selects on a given day, but it also affects how it deals with seasonal fluctuations in food availability. A deeper understanding of the nutritional values of different primate food sources found in the wild is important for practitioners concerned with habitat management and care of captive populations. This is because the choices that primates make regarding which foods to include in their daily diet, influence their health and fitness (Altmann 1998; Beehner et al. 2006).

The third objective of this thesis was:

- To investigate the influence of the spider monkeys’ nutritional strategy on the daily and seasonal nutritional states of individuals, estimate the nutritional value of different foods eaten, and interpret unusual food choices observed.

Specifically, I aimed to use my detailed field data-set on nutrient intake to assess the impact of food availability on seasonal nutritional states of individuals; which extrinsic and intrinsic factors influenced the strategies they employed to reach their daily nutrient requirements; and to assess the value of different foods in terms of the balance between protein on one hand and soluble carbohydrates and lipids on the other.

To satisfy the third objective, I analysed daily nutritional contributions of different plant species, and examined this information in relation to their seasonal availability. I evaluated different food types by relating their macro-nutritional balance to the observed ratio of macro-nutritional intake by spider monkeys. I also investigated the daily tracking between consecutive feeding events by individuals in order to describe the different strategies they employed to reach their daily nutrient requirements, e.g. choosing nutritionally-balanced foods or switching between complementary foods. I also statistically analyzed whether these strategies were influenced by factors such as habitat-wide availability of certain foods and their dominance in the diet.

1.3.4. Objective four

It is critical for forest recovery and regeneration that populations of seed dispersers are maintained and their ecological function remains intact. In Neotropical forests spider monkeys play an important role in seed dispersal (Chapman & Russo 2007). However, they also belong to a group of primate species that are especially sensitive to habitat disturbance (Skorupa 1986; Johns & Skorupa 1987; Peres 1994b; Sorensen & Fedigan 2000; Felton *et al.* 2003). Because reductions in the densities of frugivorous primates can have deleterious effects on forest recovery and regeneration (Chapman & Chapman 1996; Chapman & Onderdonk 1998), long-term sustainability of Bolivian certified forestry depends on the maintenance of viable populations of spider monkeys and other important seed dispersers.

The fourth objective in this thesis was:

- To quantify the importance of timber tree species in the diet and feeding ecology of *Ateles chamek*.

Specifically, I aimed to quantify the contribution of timber tree species to the spider monkeys' staple food group, peak season diets and fall-back diets. With that information I aimed to estimate the impacts on their food resources of timber extraction under current harvesting intensities.

I satisfied this fourth objective by analyzing the daily and seasonal nutritional contributions of timber tree species to the diet of the spider monkeys. I placed this information into the context of actual timber extraction rates from this forest and estimated the impact different timber removal rates may have on the nutritional ecology of these important seed dispersers.

1.4. Thesis structure

Chapter 1 provided an introduction to the field of primate nutritional ecology as it relates to their conservation. Chapters 2 – 5 are based on field work conducted in La Chonta, Bolivia, during September 2003 – September 2004. Because these chapters are manuscripts developed for independent publication in scientific journals, some repetition between chapters is unavoidable.

Chapter 2 describes the feeding time budget and temporal patterns of food consumption by my study community of Peruvian spider monkeys, *Ateles chamek*. A novel analysis of the spider monkeys' nutritional intakes is demonstrated in Chapter 3, where I determine the nutritional strategy that governs diet selection in these primates. Chapter 4 builds on the findings of chapters 2 and 3 and examines how the nutritional strategy of the spider monkeys influences seasonal diets and the resultant nutritional states of individuals. In that chapter I also assess the relative value of different food sources and provide explanations for the unusual food choices described in Chapter 1. In Chapter 5 I combine the results of chapters 2, 3, and 4 to determine the importance of commercial timber tree species in the diet and nutritional ecology of this community of spider monkeys. Chapter 6 concludes the findings of the thesis and provides a brief synthesis of earlier chapters. In this final chapter I also briefly discuss implications of my findings, lessons learn from this study, and recommendations for future research.

Following the concluding chapter, three tables are attached in Appendices 1 – 3. Appendix 1, which I refer to in Chapter 2, provides a table listing all food types consumed by the spider monkeys, and the relative proportion of feeding time spent on each food type. Appendix 2 and 3 are referred to in Chapter 4. The former table lists the nutritional composition of different food items consumed by the spider monkeys, and the latter provides information regarding the seasonal differences in dietary composition in terms of nutrient intakes from important food species. Prior to each chapter are photographs depicting the spider monkeys and their food resources.

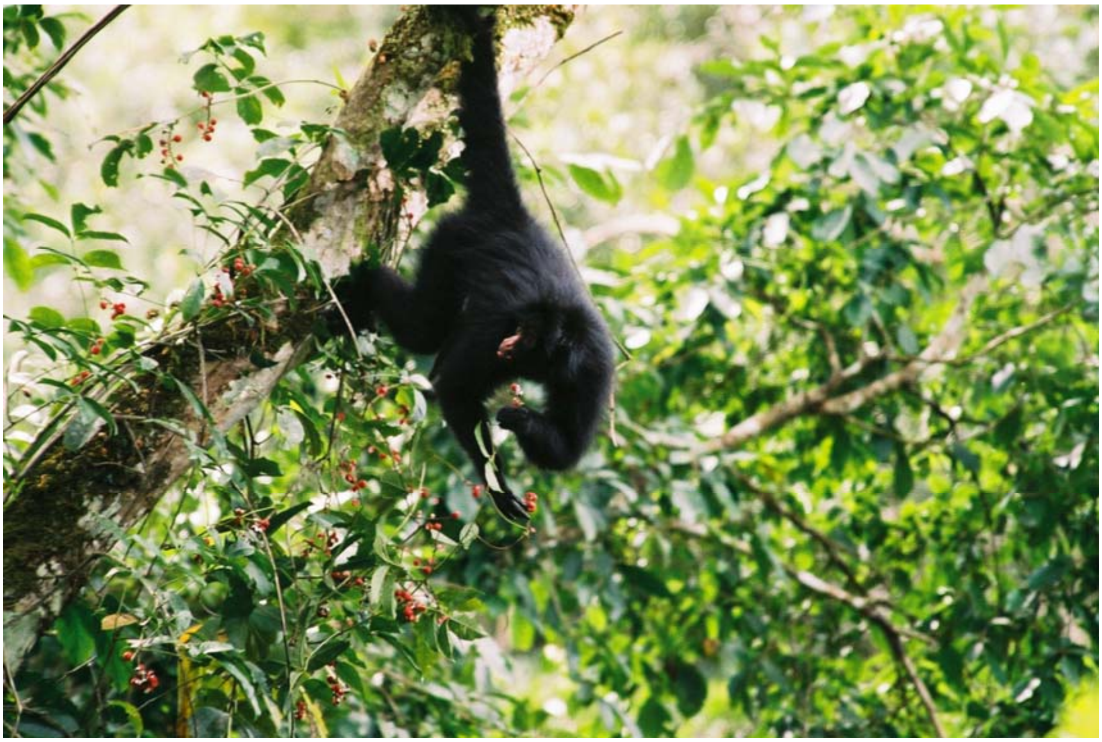

Photo by Annika Felton

Ripe fruit of the liana *Paullinia elegans* consumed by a male spider monkey.

Chapter 2 - Diet and feeding ecology of the Peruvian spider monkey (*Ateles chamek*) in a Bolivian semi-humid forest: The importance of *Ficus* as a staple food resource

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2.1. Abstract

We describe temporal patterns of food consumption by the Peruvian spider monkey *Ateles chamek* in a semi-humid forest in lowland Bolivia. Dietary composition is assessed in relation to temporal variation in abundance, duration, and synchrony of different food items in their home range. We collected data from September 2003 to September 2004, in the forestry concession La Chonta, Department of Santa Cruz. Throughout the period of detailed feeding data collection (February to September 2004), *Ateles chamek* used *Ficus* as a staple food resource. Figs comprised almost 50% of their diet in terms of total time spent feeding and were consumed to a great extent even during times of high overall food availability. This is contrary to the general expectation that for Neotropical frugivores, *Ficus* is a fall-back food in times of fruit scarcity, rather than a staple food resource. Surprisingly, *Ateles chamek* spent 18% of their feeding time eating unripe figs. This is despite these primates being considered ripe fruit specialists. *Ateles chamek* consumed unripe figs all through the year, including periods when ripe figs and other ripe fruit were abundant. We identify other important fall-back foods for *Ateles chamek* in this forest, in particular the ripe fruit of *Myrciaria* sp.

2.2. Introduction

Over the course of a year the majority of the world's tropical forests experience seasonal variation in rainfall, temperature and day length (van Schaik et al. 1993). This results in distinct and predictable periods with varying production, duration and synchrony of food resources that can be consumed by primates (van Schaik et al. 1993; Janson & Chapman 1999). During periods of relatively low abundance of their preferred food, primates must be able to alter their dietary composition and/or activity patterns, if they are to avoid negative impacts on health and reproduction (van Schaik et al. 1993).

Spider monkeys (genus *Ateles,* subfamily Atelinae) are canopy dwelling frugivores found in Neotropical forests that in many parts experience marked seasonal differences in rainfall and food availability (Di Fiore et al. in press). Spider monkeys are considered to be ripe fruit specialists, spending 75-90% of their foraging time consuming predominantly ripe fruit (Klein & Klein 1977; van Roosmalen 1985; Chapman 1987;1988; Symington 1988a; Cant 1990; Castellanos 1995; Kinzey 1997; Dew 2001; Wallace 2005). However, spider monkeys can temporarily switch to alternative diets if conditions require them to do so (Chapman & Chapman 1990). During periods of fruit scarcity, they may rely on flowers and leaves (van Roosmalen 1985; Chapman 1987; Symington 1988c), unripe fruit in combination with leaves (Milton 1993a; Wallace 2005), or rarely, on seeds (Cant 1990).

One important fall-back food for atelines during times of food scarcity is the ripe fig (syconium) produced by members of the genus *Ficus* (Terborgh 1983). *Ficus* trees are renowned for their tendency to provide food out of synchrony with the rest of the forest (Janzen 1979). Although figs are rarely preferred by primates in times of plenty (Milton et al. 1982; Shanahan et al. 2001), they are often considered to be a keystone resource due to large crop sizes, their accessibility to small as well as large primates, and their reliability in times of general fruit scarcity (Terborgh 1983;1986; Shanahan *et al.* 2001).

Descriptions of the diets of frugivorous primates have traditionally contrasted the relative importance of different food items by the time spent feeding on them. Although other methods that assess the nutritional or mineral content of the diet can be used to elucidate the motivations underlying a species' feeding ecology, time-based assessments are an excellent means of comparing study populations in different forest types and the relative dominance of different food resources in their diet. In this paper we describe the diet of a community of the Peruvian spider monkey (*Ateles chamek* Humboldt 1812) in a semi-deciduous humid forest in lowland Bolivia. Seasonal changes in diet composition are described in terms of the proportion of time spent feeding and interpreted in relation to the temporal variation in abundance, duration and synchrony of different food items in their home range. We assess the relative importance of *Ficus* in their diet and how the temporal pattern of *Ficus* use is related to the abundance of other food resources.

2.3. Methods

2.3.1. Study area and subjects

A.M. Felton conducted the field study in the lowland subtropical semi-humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia (Figure 2.1). The study area (S: 15 36 26.3 to 15 37 44.5 and W: 62 46 58.9 to 62 47 55.7) was located in the 100,000 hectare forestry concession "La Chonta", which is owned and managed by Agroindustría Forestal La Chonta Ltda. The forest varies in altitude from 230 m to 390 m with an average elevation of 320 m. The area is a continuation of the Brazilian Shield with low fertility soils consisting of oxisols, ultisols, and inceptisols (Park et al., 2005). Average annual precipitation for La Chonta is 1570mm and average annual temperature is 25°C. Between November 2003 and October 2004 La Chonta received 1628mm of rainfall. The seasonal distribution of rainfall during the study was representative of the average monthly rainfall for the forest, with the possible exception of the end of the dry season when rainfall was below average (Figure 2.2). The study area was situated approximately 5km from the northern edge of the concession and at least 2 km from recent logging disturbance (harvesting 2001-2002). The closest active timber harvesting was at least 8 km to the west of the study area and was not audible to the researchers.

The Peruvian spider monkey *Ateles chamek* is the most abundant primate species in this section of the Guarayos Forest Reserve (Wallace et al. 2000). Four other primate species occur in La Chonta: *Alouatta* cf. *seniculus, Aotus azarae, Callithrix melanura* and *Cebus apella.* Species of *Ateles* live in fission-fusion societies in which individuals from a large community associate on a daily basis in small subgroups that change size and membership frequently (Di Fiore & Campbell 2007). Our study community consisted of 55 individuals at the end of the study period.

2.3.2. Study design and vegetation survey

During habituation of the study community (duration of five months) we established a network of trails (40 km in total) in the study community's home range, which covered an area of approximately 360-400ha. We used this network for daily follows, monthly phenology surveys and a one-off vegetation survey. We collected phenology data within 5m of each side of these trails and additional trails immediately abutting the home range (total length 56km). Phenology methods are detailed below. To describe the vegetation in the home range and to obtain basal area information of monitored food species, at the end of the study period we established 71 vegetation plots (100m long, 10m wide). We distributed plots within the trail network in relative proportion to the different vegetation types that we had visually categorized during the course of the year. In these plots all trees ≥10cm diameter at breast height (dbh) were identified and their diameter measured.

2.3.3. Phenology survey

In the survey population we included plants belonging to plant genera known or presumed to be eaten by *Ateles*. When possible we included at least 30 individuals of each species in the survey, selected randomly along survey trails. We initially tagged trees of ≥10cm dbh, mature palms and lianas, and then monitored them approximately once a month to coincide with the completion of focal animal follows. We collected phenology data from November 2003 to October 2004. Due to severe storms we did not collect data in January. During each survey we noted the presence of ripe fruit, immature fruit and flowers. We used differences in fruit size, color and consistency to differentiate between immature and ripe fruits. From here on we use the term "unripe" and include fruit ranging from emerging fruit (very small and green) to fruit of mature size but not of ripe coloration or texture.

Because the contribution of different species in the phenology survey did not represent their actual densities in the forest, we had to calibrate monthly food availability estimates (Chapman, Wrangham & Chapman 1994). Because the basal area of a tree is an easy and reasonably accurate index of its fruit crop sizes (McDiarmid, Ricklefs & Foster 1977; Leighton & Leighton 1982; Peters *et al.* 1988), we used basal area information to calculate a monthly index of general food availability. We calculated species-specific basal area values as a mean for the entire home range, averaging across the three vegetation types according to their relative contribution. For dioecious tree species, such as *Pseudolmedia laevis* and 25 other species in the study area; (Kubitzki & Kurz 1984; Bawa, Perry & Beach 1985; Bawa & Krugman 1991; Justiniano *et al.* 2003; Mostacedo *et al.* 2003; Ressell *et al.* 2004), we assumed that half of the present trees were female and produced fruit (as per Fredericksen et al. 1999). For trees, we calculated a monthly index T:

$$\text{Index T} = \sum_i (p_i \times BA_i)*100$$

where p_i is the proportion of surveyed individuals of species *i* that carry an edible pheno-phase at a given time, and BA_i is basal area/ha of species *i*. We also broke down Index T into different categories: ripe fruit, unripe fruit, ripe figs, unripe figs and flowers. Due to the relatively long interval between surveys (approximately 30 days), we did not observe the fate of some documented unripe fig crops as they had ripened and been eaten by animals before the subsequent survey. For this reason, we have estimated the date when these ripe crops would have been available by arbitrarily choosing the mid-point between consecutive surveys. We present these data points as “projected” data. We did this only for *Ficus* species, as this genus is treated separately for the purpose of this paper. In the general tree fruit index, we include many species and the effect of unripe crops with undocumented fate will be smaller.

Because the trunks of arboreal palm trees generally do not grow incrementally (Schatz et al. 1985), we did not measure their diameter and could therefore not include them in index T. Instead we calculated a separate index “P” of palm food availability based on their densities:

$$\text{Index P} = \sum_i (p_i \times d_i)*100$$

where d_i is density of species *i* (individuals/ha). We included a tree or palm species in index T or P if it 1) was recorded as an *Ateles chamek* food source during the study, 2) was included in the phenology trail and 3) was present in the vegetation survey plots to supply basal area or density information. We did not include lianas in the vegetation survey, so no abundance data was available. For liana species recorded to be *Ateles chamek* food sources during the study, we therefore calculated a simple monthly index of percentage of surveyed lianas bearing ripe fruit (index L).

2.3.4. Feeding observations

We identified and measured (dbh) all observed feeding trees of *Ateles chamek* between September 2003 and September 2004. Following habituation, we systematically collected detailed feeding data from February 2004 to September 2004. Because the unit of interest for this study was the food intake per individual per day, we conducted continuous observations of the same focal individual from dawn (5:45-6:15 h) to dusk (17:45-18:30 h). We established a list of 18 readily identified focal animals (FA). Individuals were identified by facial and bodily markings. Eight of these were adult males and ten were adult females that were lactating or pregnant, as well as caring for a dependent juvenile. When possible, we followed 10-15 of these individuals for one whole day each month, over a period of 20 days, and alternated between male and female FAs on a daily basis. Days when the FA was successfully followed for >10hrs we refer to as "full". Days when the FA was followed <10hrs the day (minimum of 5hrs) we refer to as "partial".

We collected data continuously on the FA's activities, including even short feeding events. We noted the exact start and end time of each feeding session (event). We recorded the plant parts eaten: ripe fruit/ fig, unripe fruit/ fig (separated into emerging, young and mature fruit), flower, young leaf, mature leaf, or other. Near-ripe fruit and figs were included in the ripe category. We identified and tagged all plants that either the FA or other members of the subgroup were eating from.

2.3.5. Data analysis

We calculated proportions of dietary items and plant species based on the total amount of time spent feeding by focal animals. We excluded partial follow days with less than 60 minutes of feeding observations from these percentages (daily feeding time of full days averaged 155min, range 52-303min).

We calculated an electivity index (E_i) to determine food species preference in the *Ateles chamek* diet. The index is calculated as follows (Krebs 1989):

$$E_i = (r_i - n_i)/(r_i + n_i)$$

where r_i is the percentage of species *i* in the diet (based on time spent feeding), and n_i is the relative abundance of species *i* in the spider monkey home range (based on basal area/ha). We adjusted basal area values for dioecious species. Index values range from -1 (avoided) to +1 (highly selected).

We tested whether there was a statistical difference between months in time spent feeding by FA observed during full days, using linear regression analysis, including sex of the FA as a predictor. To assess whether different aspects of food availability were driving daily time spent feeding by FA observed during full days, we ran regression models using the following candidate variables: availability of ripe figs, unripe figs, ripe non-fig fruit, unripe non-fig fruit, flowers, and the sex of the FA. We matched daily data on time spent feeding with the food availability indices produced from phenology surveys conducted on dates (within two weeks) closest to the follow days. We selected regression models by considering all possible subsets of predictors and then choosing the model with the smallest value for the Akaike Information Criteria (Akaike 1974). We ran two similar regression analyses with "time spent feeding on figs in total" and "time spent feeding on ripe figs" as response variables, with the same candidate variables as listed above. We checked for departures from our assumptions by inspecting QQ plots of residuals, and plots of residuals against fitted values. All full follow days were treated as independent data points, because the estimated correlation between follow days for the same animal was negative and negligible.

2.4. Results

2.4.1. Vegetation structure in home range

The study community's home range was primarily tall forest (approximately 60% of study area), with smaller areas of low vine forest (35%) and chaparral (<5%) and swamp (<1%). The tall forest is characterized by greater tree density, basal area and mean height of trees than the low forest and the chaparral (Table 2.1). The three vegetation types are further categorized by having different dominant tree species (Table 2.1).

2.4.2. Phenology

We initially included 2105 individual plants in the monthly phenology surveys. During the year we excluded 103 plants because they died or their canopies could not be properly observed from the ground. Seventy-two species of trees and 20 species of lianas were represented. Of these 92 species, we observed 44 to be used by *Ateles chamek* during the year: 34 species of trees and 10 species of lianas. During the year *Ateles chamek* also fed from 11 additional plant species that were not included in the surveys (one major food source (*Heliocarpus americanus* L., Tiliaceae) and ten minor food species). The fruiting periods of the species included in surveys are presented in Appendix 1.

The seasonal changes in food availability from November 2003 to October 2004 are shown in Figure 2.3. When phenology surveys began in the wet season ripe fruit were abundant. In early February we detected paucity in fruit abundance (Figure 2.3). During the period of detailed feeding data collection (Feb-Sep) three distinct phenological periods can be detected (Table 2.2). A period of relatively high ripe fruit abundance occurred during the late wet season. Following this period there were 10-14 weeks of tree fruit scarcity during the early-to-mid dry season. The second half of this period was particularly poor in ripe fruit when neither trees nor lianas provided many ripe crops in the home range. During this time *Myrciaria* sp. (local name "sahuinto") was the primary source of ripe fruit in the home range. This species also fruited during the short period of general fruit scarcity in early February. After the long period of fruit scarcity, ripe fruit was abundant again during the late dry-to-early wet season.

During the study, lianas had one period of ripe fruit production that occurred with a month's time lag to trees (Figure 2.4). Palms provided ripe fruit at an almost continuous level throughout the study period, with peaks overlapping with periods of high tree fruit abundance (Figure 2.4). Unripe figs (Figure 2.3) and edible unripe non-fig fruit were also available continuously throughout the year.

Of the four *Ficus* species in the phenological survey, *Ficus boliviana*[1] and *F. trigona* represented 91% of available crops. *Ficus* species periodically provided ripe fruit when other trees did not (indicated in Figure 2.3). However, during the two observed dips in general tree fruit availability, ripe fig availability also declined

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[1]. The taxonomy of this species is uncertain at the time of printing. This species may be *Ficus insipida* (synonym *F. glabrata*), but because the name *F. boliviana* is the accepted classification employed by Bolivian researchers I have chosen to use it throughout the thesis. Please contact the author for updated nomenclature.

(Figure 2.3). When ripe fig crops are projected from observed unripe crops with unknown ripening date (see methods), only 2-6 additional trees presented ripe crops during the long period of fruit scarcity. In comparison, 10-13 additional ripe fig crops occurred during the late dry-to-early wet season (Aug-Sep). During the fruit-poor months of late May and June, the scarcity of ripe figs corresponded with a similar lack of ripe figs in the diet of *Ateles chamek*. This suggests that the sample of fig trees in our survey was representative for the community's home range in general.

During the months of data collection on feeding, the two dominant *Ficus* species (*F. trigona* and *F. boliviana*) both showed a bimodal fruiting pattern that overlapped in time with each other. Both species peaked in fruit production in early May and late August to October.

2.4.3. *Ateles chamek* feeding observations

From February to September, we conducted 863 hours of focal animal observations. During this time we recorded 904 different feeding events for FAs, ranging in duration from 0.2min to 204min, and amounting to 175 hours of feeding observation (collected during 32 full and 11 partial follow days for females; 19 full and 8 partial follow days for males). Time spent feeding by FA during full follow days differed significantly between months and sexes (combined model: adjusted R^2=46.4, month $p<0.001$, sex $p<0.001$). July and August had the highest recorded daily feeding time (mean 180min/ day ± 11min), while late May and June had the lowest (mean 100min/day ± 14min). Females spent more time feeding than males (females: mean 169min/day ± 10min; males: mean 132min/day ± 12min).

2.4.4. Overall diet

Feeding data of *Ateles chamek* reveal that fruits constituted 82% of the total diet in terms of time spent feeding (Appendix1). Focal animals spent 39.3% of the fruit feeding time on ripe non-fig fruit, 32.7% on ripe figs, 6.2% on unripe non-fig fruits, and 17.8% on unripe figs. For focal animals, leaf material constituted 13% of the total feeding time, where most of this was represented by leaf buds (52% of leaf consumption time) and young leaves (26%). Flowers were a seasonal food for *Ateles chamek* and amounted to 4.7% of total feeding time. They also consumed other vegetative material such as palm heart, dead wood, aerial roots, stalks and bark. These items made up only 0.2% of all feeding time (Appendix1). We also observed invertebrates being consumed on 8 occasions (<1% of feeding events). Five of these events occurred during habituation when *Ateles chamek* were observed to feed for long periods of time on caterpillars occupying the leaves of *Terminalia oblonga*.

2.4.5. Dietary diversity and prominent plant species in feeding time budget

During the 12 months of data collection on food sources, we observed *Ateles chamek* to eat 105 different types of plant items, belonging to 63 species, representing 37 families (Appendix1). In the diet of focal animals, Moraceae was the family represented with most species. In terms of time spent feeding, Moraceae also topped the list (61.2% of total feeding time).

The fruits of just two tree species comprised almost 50% of their total time spent feeding. The tree species upon whose fruits they spent the most time feeding were *Ficus boliviana* (28.6% of time), *F. trigona* (20.3%), *Myrciaria* sp. (10.3%) and *Pseudolmedia laevis* (9.4%; Appendix1). *Ficus* was absent from the diet in only 8 of the 51 full follow days, 7 of those occurred during the period of fruit scarcity in June.

In terms of time spent feeding ripe fruit, the primary source was *Ficus trigona* (30.2% of time spent eating ripe fruit) followed by *Myrciaria* sp. (17.4%) and *F. boliviana* (14.5%; Appendix1). Palm fruit constituted only 2% of time eating ripe fruit. The equivalent value for liana fruit was 7.6%. Of the time spent feeding on unripe fruit, 68.1% was spent in *Ficus boliviana*. Besides *Ficus boliviana*, FAs ate unripe fruit mainly from *Pouteria nemorosa* (11.9%: medium-ripe fruit), *Pseudolmedia laevis* (9.7%: emerging and young fruit), and *F. trigona* (8.7%: small immature figs; Appendix 1). The medium-ripe fruit FAs harvested from *Pouteria nemorosa* were from trees that appeared to have a damaged crop of fruit the year of sampling: fruits were water laden and rotting on the branch, did not fully ripen and were often rejected by monkeys.

The time FAs spent eating figs was almost equally divided between the two most common species of *Ficus* in the forest: 48.2% for *F. boliviana*, and 50.1% for *F. trigona*. The remaining portion of total fig eating time FAs spent in three rare *Ficus* species (*F. eximia, F. pertusa,* and *F. gomelleira*). Notably, 65% of time they spent eating figs in *Ficus boliviana* was on unripe figs, while the equivalent value for *F. trigona* was 10%. *Ficus boliviana* was the source of 87.8% of time spent feeding unripe figs in general.

The majority of the time FAs spent eating young leaves were in *Ficus* (*F. boliviana* 43.4%, *F. trigona* 4.7%). The plant species that provided most flowers and flower buds was *Pseudolmedia laevis* (84.7% of flower feeding time; Appendix1).

The relative importance of eleven other species, which are known food or presumed sources for *Ateles* (*Alibertia verrucosa, Ampelocera ruizii, Attalea phalerata, Brosimium guadichaudii, Cordia alliodora, Dendropanax arboreus, Didymopanax morototoni, Guarea guidonia, Inga edulis, Syagrus sancona,* and *Talisia esculenta;* Wallace, 1998; pers. obs.), may have been underestimated as their fruiting period overlapped only partially or not at all with behavioral data collection. Due to the damaged crop of *Pouteria nemorosa* during the study period (see above) this species is potentially underestimated as well.

2.4.6. Feeding preferences

For comparison with other studies, we present preference results at the genus level (Table 2.3). However, as most genera in this study are represented by only one species we will interpret results at the species level in the text. The locally rare *Virola sebifera* has the highest Electivity Index (EI), followed by *Myrciaria* sp. and *Batocarpus amazonicus* (Table 2.3). *Ficus boliviana* also has a high EI and is ranked as number 7 of the 29 genera included. *Jacaratia spinosa* and *Didymopanax morototoni* were used in accordance to their abundance in the forest (EI close to zero), while several species which were sources of leaves, were fed upon less often than expected relative to their abundance (Table 2.3). Only one palm species had a positive EI (*Syagrus sancona*) even though FAs only ate its flowers. Fruit-providing palms had EIs close to zero (Table 2.3).

2.4.7. Seed handling

Focal animals were observed to ingest whole seeds and defecate them intact in 98% of feeding events. The exceptions were three large-seeded palm species (*Socratea exorrhiza, Astrocaryum murumuru,* and *Attalea phalerata*). *Ateles chamek* systematically spat out palm seeds when feeding on the ripe pulp. In no instance did we observe mastication of seeds. In some cases *Ateles chamek* ingested small emerging fruit whose seeds may have been vulnerable to digestion due to their immaturity (*Ficus boliviana* 3.8% of fruit/fig feeding time; *F. trigona* 0.5%; and *Pseudolmedia laevis* <0.1%).

2.4.8. Monthly changes in dietary composition

The relative proportions of dietary items varied among months (Figure 2.5). Fruit and figs contributed >70% of the diet in all months except June (53%). In June *Ateles chamek* fed more on leaves and flowers than in other months. The proportion of figs in their diet varied from 2% to 73% (Figure 2.5). Unripe fruit/figs constituted >10% of the feeding time in five of the eight months of detailed data collection, and was >40% in two months (March 43%, May 45%). The proportion of leaf material in their diet varied from 0 % to 32% (Figure 2.5). Flower consumption varied from 0% to14% of monthly feeding time, with the peak overlapping with that of leaf consumption (June).

The food sources that contributed to at least 5% of the monthly diet in terms of time spent feeding are listed in Table 2.4. Two to six species each month qualified to be included, and the time spent feeding on these top species amounted to 82% to 96% of the monthly diets. *Ficus boliviana* tops the list as being prominent in six of the eight months of detailed data collection (Table 2.4).

2.4.9. Feeding in relation to availability

Daily time spent feeding by focal animals was best explained by three significant variables (best regression model included 3 terms): availability of ripe figs, unripe figs, and the sex of the focal animal (Combined model: adjusted R^2=34.6, ripe figs p=0.005, unripe figs p=0.009, sex p=0.002). Hence, the availability of mainly two *Ficus* species influenced the daily feeding time more strongly than the availability of 25 other fruiting plant species.

Daily time spent feeding on figs in total (ripe and unripe) was best explained by the availability of ripe figs (best regression model included 1 term: adjusted R^2=50.7, ripe figs p<0.001). The same model revealed that there was no significant difference between sexes in time spent feeding on figs in total (p=0.208). The difference between sexes in overall feeding time can instead be explained by females spending significantly more time than males feeding on ripe figs (best regression model included 3 terms, adjusted R^2=26.6, ripe figs p=0.009, unripe fruit p=0.026, sex p=0.038).

There was no inverse relationship between fig consumption and general ripe fruit availability, as may be expected if figs were merely a fall-back food consumed in times of general fruit scarcity. Instead, the second of the two peaks in fig consumption overlapped with the peak in ripe non-fig fruit availability in the late dry – early wet season. Contrary to expectations, unripe figs (out of which the majority was *Ficus boliviana*) were consumed during times of both abundance and scarcity of ripe *F. boliviana* (Figure 2.6). The second peak in consumption of unripe figs occurred when ripe non-fig fruits were abundant (July - Aug). Similarly, the consumption of young leaves was high during this rich period, when young leaves were harvested mainly from fig trees and lianas. Mature leaves on the other hand were primarily eaten during the fruit scarce period.

2.4.10. Fall-back foods during period of fruit scarcity

During the long period of general fruit scarcity (early-to-mid dry season), *Ateles chamek* consumed ripe fruit of *Myrciaria* sp. (Table 2.4). *Ateles chamek* fed on items of *Ficus* only in the beginning of this period (ripe figs of *F. trigona* and unripe figs and leaf buds of *F. boliviana*), when they also consumed ripe fruit from the liana *Celtis iguanea*. To supplement the *Myrciaria* diet during the rest of the period, *Ateles chamek* consumed young leaves and leaf buds of *Batocarpus amazonicus*, mature leaves of *Heliocarpus americanus* and flower buds of *Pseudolmedia laevis*.

Table 2.1. Vegetation structure of the three main forest types in the home range of the *Ateles chamek* study community at La Chonta (plot means ± 1 standard error). Numbers in parentheses indicate approximate contribution of each forest type within the home range. Eight plots that contained a mixture of different forest types are not included in this table.

Mean of plots	**Tall forest (60%)**	**Low forest (35%)**	**Chaparral (5%)**
# plots surveyed	39	22	2
Tree density (# trees/ha)	491 ± 15	394 ± 23	385 ± 5
Basal area (m^2/ha)	29.8 ± 2	20.3 ± 1.9	20 ± 3.1
Height (m)	12.4 ± 0.3	10.5 ± 0.3	10.1 ± 0.2
Liana infestation index (0-3)	1.4 ± 0.1	1.8 ± 0.4	1.7 ± 0.6
Species diversity	20.4 ± 0.8	19.8 ± 0.8	20.5 ± 2.5
Dominant species (density)	*Pseudolmedia laevis* (Moraceae) *Ocotea* sp (“laurel”, Lauraceae) *Socratea exorrhiza* (Arecaceae)	*Ampelocera ruizii* (Ulmaceae) *Gallesia integrifolia* (Phytolaccaceae) *Terminalia oblonga* (Combretaceae)	*Cariniana ianeirensis* (Lecythidaceae) *Schizolobium parahyba* (Ceasalpiniaceae) *Ceiba pentandra* (Bombaceae)
Dominant species (basal area)	*Pseudolmedia laevis* (Moraceae) *Hura crepitans* (Euphorbiaceae) *Ficus trigona* (Moraceae)	*Pseudolmedia laevis* (Moraceae) *Urera baccifera* (Urticaceae) *Pouteria macrophylla* (Sapotaceae)	*Urera baccifera* (Urticaceae) *Pseudolmedia laevis* (Moraceae) *Ocotea* sp. ("negrillo", Lauraceae)

Table 2.2. Description of three phenological periods during the period of detailed data collection of *Ateles chamek* feeding behaviour in La Chonta, February to September 2004.

	Late wet	Early-mid dry	Late dry- early wet
Months	Feb to mid-Apr	Mid-Apr to early July	Early July to mid-Sep
# of surveys conducted	3	3	2
Mean phenology score of all ripe tree fruit[1]	38 (50)**	22	48
Range of scores between surveys	14-52	10-41	43-53
Major sources of ripe fruit available[1,2]	*Spondias mombin* *Pouteria nemorosa* (a) *Jacaratia spinosa* *Ficus boliviana* (b) *Inga edulis* *Alibertia verrucosa* *Myrciaria* sp. *Ampelocera ruizii* *Sapium glandulosum*	*Myrciaria* sp. *Ficus trigona* (c) *Ficus boliviana* (c)	*Dendropanax arboreus* *Ficus trigona* *Guazuma ulmifolia* *Myrciaria* sp. *Ficus boliviana* *Didymopanax morototoni* *Pouteria macrophylla*

** Value in parenthesis: mean score when the low value of February is excluded. [1] Phenology index T (see Methods for explanation of score calculation).

[2] Species listed in order of abundance. a) End of February only; b) Large peak at the end of period; c) At the beginning of period only.

Table 2.3. Electivity indices for genera included in the diet of *Ateles chamek* in La Chonta.

Family	Genus	Cat.[a]	#spp[b]	BA/ha[c]	%BA/ha[d]	EI[e]	EI rank	T Rank[f]
MYRISTICACEAE	*Virola*	T	1	<0.01	0.02	0.91	1	22
MYRTACEAE	*Myrciaria*	T	1	0.17	0.63	0.88	2	3
MORACEAE	*Batocarpus*	T	1	0.07	0.26	0.78	3	9
TILIACEAE	*Heliocarpus*	T	1	0.07	0.26	0.81	4	10
STERCULIACEAE	*Guazuma*	T	1	0.13	0.48	0.76	5	7
ARECACEAE	*Syagrus*	P	1	3.54	0.78	0.61	6	30-33
MORACEAE	*Ficus**	T	3	3.33	12.70	0.59	7	1, 2, 27
MIMOSACEAE	*Inga*	T	1	0.10	0.37	0.57	8	13
EUPHORBIACEAE	*Sapium*	T	1	0.18	0.69	0.36	9	12
ARALIACEAE	*Dendropanax*	T	1	0.32	1.22	0.31	10	8
SAPOTACEAE	*Pouteria*	T	1	0.59	2.26	0.29	11	5
ANACARDIACEAE	*Spondias*	T	1	0.35	1.32	0.19	12	11
CARICACEAE	*Jacaratia*	T	1	0.35	1.34	-0.03	13	14
ARALIACEAE	*Didymopanax*	T	1	0.04	0.14	-0.05	14	27-29
ARECACEAE	*Attalea*	P	1	1.13	0.25	-0.08	15	24
ARECACEAE	*Astrocaryum*	P	1	2.33	0.52	-0.14	16	20
MORACEAE	*Pseudolmedia*	T	1	4.42	16.85	-0.29	17	4
SAPINDACEAE	*Talisia*	T	1	0.03	0.10	-0.46	18	38-40
CECROPIACEAE	*Cecropia*	T	1	0.02	0.06	-0.50	19	43-44
CHRYSOBALANACEAE	*Hirtella*	T	1	0.07	0.28	-0.53	20	30-33
MALVACEAE	*Ceiba*	T	2	0.32	1.23	-0.70	21	25, 50
RUBIACEAE	*Alibertia*	T	1	0.08	0.30	-0.82	22	41-42
MORACEAE	*Brosimum*	T	1	0.11	0.40	-0.83	23	38-40
ARECACEAE	*Socratea*	P	1	25.29	5.60	-0.85	24	19
URTICACEAE	*Urera*	T	1	0.49	1.85	-0.87	25	27-29
ULMACEAE	*Ampelocera*	T	1	1.58	6.04	-0.91	26	23
RUTACEAE	*Zanthoxylon*	T	1	0.08	0.30	-0.92	27	45-49
COMBRETACEAE	*Terminalia*	T	1	1.67	6.35	-0.97	28	30-33
CAESALPINIACEAE	*Caesalpinia*	T	1	0.31	1.20	-0.98	29	45-49

a) Category of food source: T=tree; P=palm. b) Number of species included; c) Basal area m^2/ha; d) Percentage of the total basal area recorded in vegetation survey. For palms, density and %density are shown and used instead of basal area; e) Electivity Index (see Methods for explanation); f) Rank according to % of total time spent feeding, listed in Appendix 1; * On a species basis*, Ficus boliviana* ranks #6, *F. trigona* #9 and *F. pertusa* # 23. No basal area information was available for other rare *Ficus* species.

Table 2.4. Plant species that contributed to ≥5% of monthly diets in terms of time spent feeding.

Family	Scientific name	Percentage of monthly diet								
		FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	# months[a]
		Late wet season			Early-mid dry season		Late dry- early wet season			
MORACEAE	*Ficus boliviana*	20	-	7	40	-	41	18	74	6
MORACEAE	*Ficus trigona*	-	-	32	22	-	5	46	-	4
MORACEAE	*Pseudolmedia laevis*	-	-	-	-	26	10	18	-	3
MYRTACEAE	*Myrciaria* sp.	-	-	-	13	42	13	-	-	3
ANACARDIACEAE	*Spondias mombin*	-	6	27	-	-	-	-	-	2
SAPOTACEAE	*Pouteria nemorosa*	16	64	-	-	-	-	-	-	2
TILIACEAE	*Heliocarpus americanus*	-	-	-	5	8	-	-	-	2
ARALIACEAE	*Dendropanax arboreus*	-	-	-	-	-	8	-	-	1
ARECACEAE	*Astrocaryum murumuru*	-	-	6	-	-	-	-	-	1
BIGNONIACEAE	*Melloa quadrivalvis*	-	-	-	-	-	-	-	12	1
CARICACEAE	*Jacaratia spinosa*	-	-	10	-	-	-	-	-	1
EUPHORBIACEAE	*Sapium glandulosum*	53	-	-	-	-	-	-	-	1
MIMOSACEAE	*Inga edulis*	-	24	-	-	-	-	-	-	1
MORACEAE	*Ficus eximia*	7	-	-	-	-	-	-	-	1
MORACEAE	*Batocarpus amazonicus*	-	-	-	-	16	-	-	-	1
SAPINDACEAE	*Paullinia elegans*	-	-	10	-	-	-	-	-	1
STERCULIACEAE	*Guazuma ulmifolia*	-	-	-	-	-	14	-	-	1
ULMACEAE	*Celtis iguanea*	-	-	-	15	-	-	-	-	1
	% of monthly diet[b]	96	94	93	96	93	92	82	86	

a) Number of months when the species contributed to >5% of the total time spent feeding. b) Percentage of monthly diet made up of the above listed species.

Table 2.5. Dietary composition data from 13 *Ateles* studies. All percentages are of total time spent feeding.

#	Species	% Fr	Monthly range	% R	%U	%S	%L	%F	%O	%Fi	%Ufig	# Fi spp	# M>5%U	Major lean season resources
1	*A. geoffroyi*	78	14-100	78	-	e	11.1	9.8	1.3	29	-	1	0	Flowers and leaves
2	*A. geoffroyi*	57	31-84	57	10[d]	19.5	14.1	1.5	-	7.8[f]	0	3	-	Seeds and ripe figs
3	*A. geoffroyi*	82	69-91	82	-	1[a]	17.2	1	0.6	6.1[h]	-	8	-	-
4	*A. paniscus*	83	54-92	80	3.3	3.1	7.9	6.4	2.7	0.95	-	10	0	Flowers and young leaves
5	*A. belzebuth*	84	78-100	83	0.8[b]	0	7	<0.1	10	3.4	-	-	0	Palm fruit
6	*A. belzebuth*	-	74-100	89	3.2[c]	-	8.3	0	3.2	9.2	-	8	0	Leaves
7	*A. belzebuth*	87	64-100	87	[g]	1.1	9	1	0.7	0.9	0	5	0	No pronounced lean season
8	*A. belzebuth*	79	52-92	-	[i]	0.8[a]	7.7	3.2	10.3	<1[h]	0	5	0	No pronounced lean season
9	*A. belzebuth*	74	55-80	72	-	2[a]	12	5	9	16.5[h]	-	8	0	Young leaves
10	*A. belzebuth*	73	41-96	-	-	-	13	12	1.2	8.1[h]	-	9	-	-
11	*A. chamek*	86	63-98	81	2.7	2	10.7	2.9	0.6	10.7	0.1	6	2	Seed and leaves
12	*A. chamek*	75	54-99	75	-	-	-	-	-	-	-	-	-	Leaf flush, flowers, figs and seeds
	AVERAGE:	78		78	4.0	3.7	10.7	3.9	4.0	8.5	0.0	6		
13	*A. chamek*	83	53-100	59	23	0	13	4.7	0.3	49.5	18	6	7	Leaves, flowers and unripe fruit/figs

Fr=fruit total; R=Ripe fruit; U=Unripe fruit pulp; S=Seed; L=Leaves; F=Flowers; O=Other; Fi=*Ficus* total; Ufig=Unripe figs;# Fi spp=Number of *Ficus* species in diet; #M>5%U=Number of months with >5% of feeding time represented by unripe fruit in general; - = no information available.

Notes: a) % of plant species; b) 1/100th of ripe fruit consumption; c) Unripe fruit included in "Other" but cannot be separated; d) approximate, calculated from data in original paper; e) Some seed included in "fruit" fraction but cannot be separated; f) Average for the main study period. Periodical means particularly for dry season diets range 14-45%; g) Not quantified rare events involving Aracaeae (1sp) and Sapotaceae (1sp); h) data from (Di Fiore et al. in press); i) Not quantified event involving Aracaeae (1sp). Source, study location and duration: 1) Santa Rosa N. P., Costa Rica, 24 months (Chapman 1987;1988); 2) Tikal N. P., Guatemala, 9 months (Cant 1990); 3) Barro Colorado Island, Panama, 14 months (Di Fiore et al. in press); 4) Voltzberg Nature Reserve, Surinam, 26 months (van Roosmalen 1985); 5) La Macarena N.P, Colombia, 11 months (Klein & Klein 1977);6) Ilha de Maraca, Brazil, 22 months (Nunes 1998); 7) Yasuni N.P, Ecuador, 12 months (Dew 2001;2005); 8) Yasuni N.P, Ecuador, 14 months (Suarez 2006); 9) Tinigua N.P, Colombia, 12 months (Stevenson et al. 2000); 10) Tinigua N.P, Colombia, 13 months (Di Fiore et al. in press); 11) Noel Kempff N.P., Bolivia, 11 months (Wallace 2006); 12) Manu N.P., Peru, 21 months (Terborgh 1983; Symington 1988c); 13) This study.

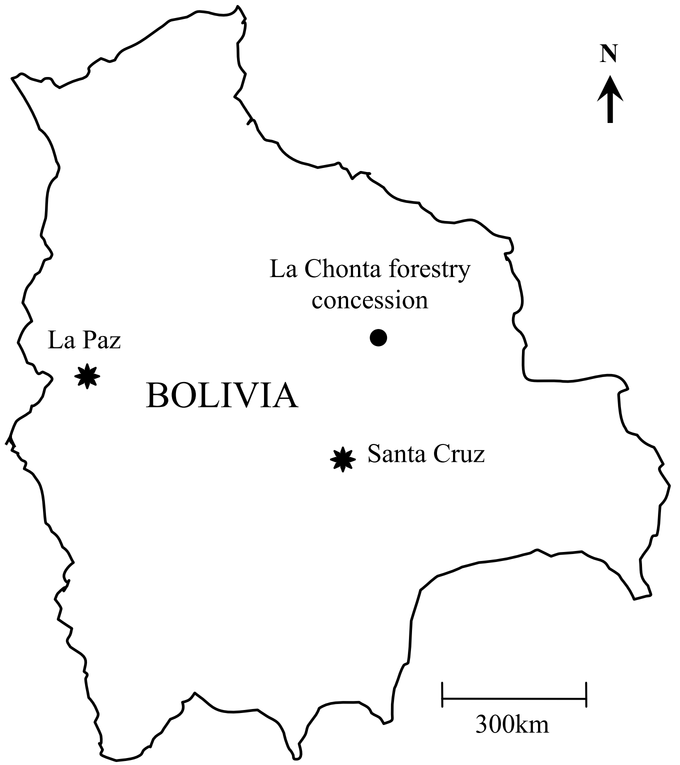

Figure 2.1. Map of Bolivia with approximate location of the La Chonta forestry concession indicated within the department of Santa Cruz, Bolivia. The La Chonta concession is approximately 300 km north of the lowland capitol city Santa Cruz.

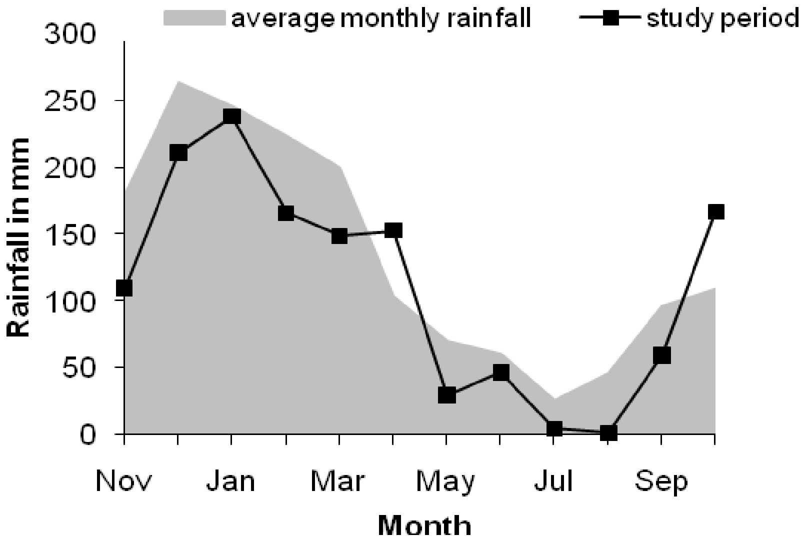

Figure 2.2. Average monthly rainfall for the La Chonta forestry concession, and specific rainfall data for study period. Data obtained from Agroindustría Forestal La Chonta Ltda.

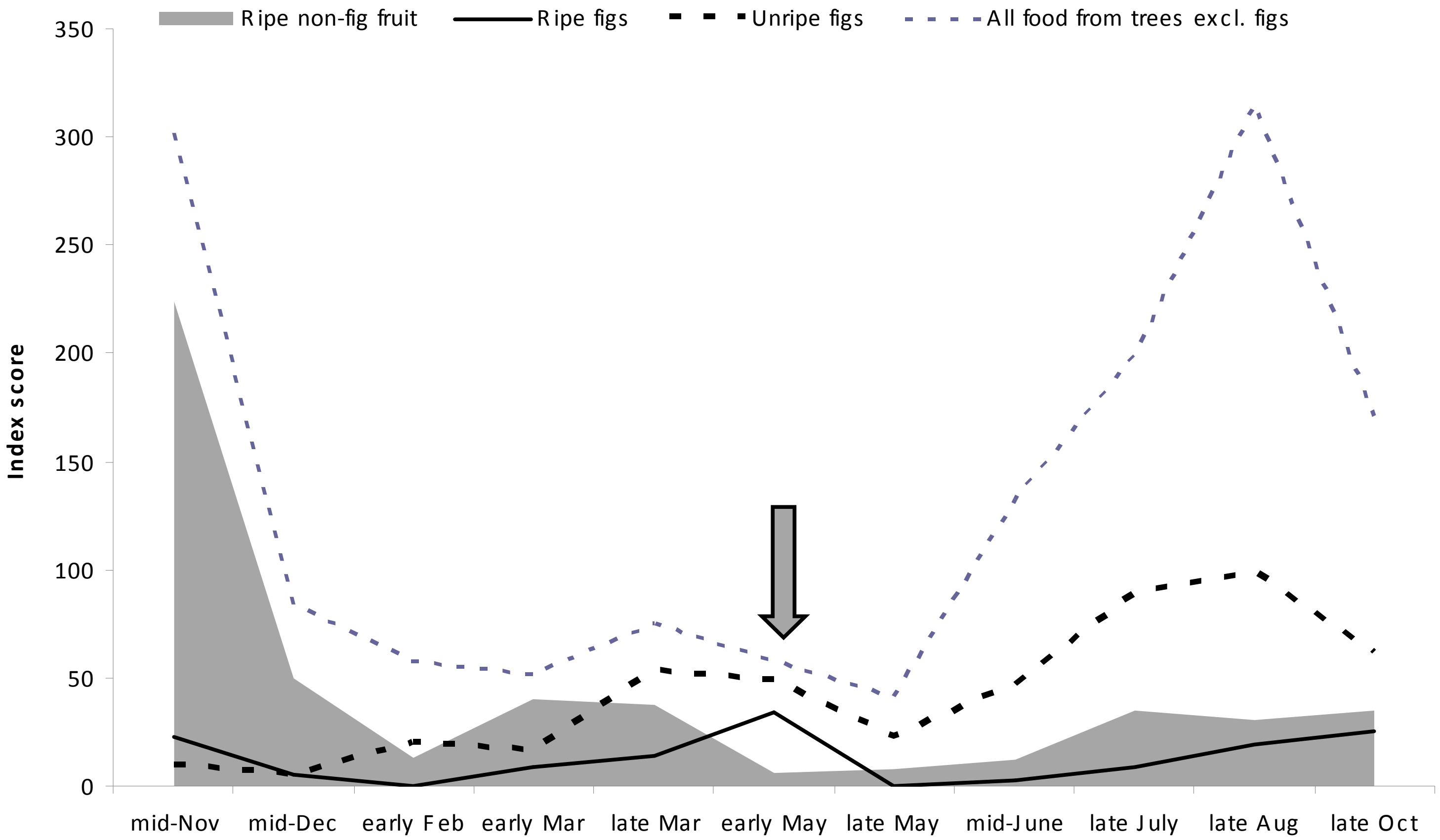

Figure 2.3. The availability of spider monkey food items from tree species in La Chonta, November 2003 to October 2004. Thirty-one tree species are included (see methods for index score explanation). "All food from trees excl. figs" includes edible flowers, ripe and unripe fruit. Grey arrow indicates period of asynchronicity in availability of ripe figs versus ripe non-fig fruit. Lines under graph indicate periods of ripe non-fig fruit scarcity when ripe figs were also scarce.

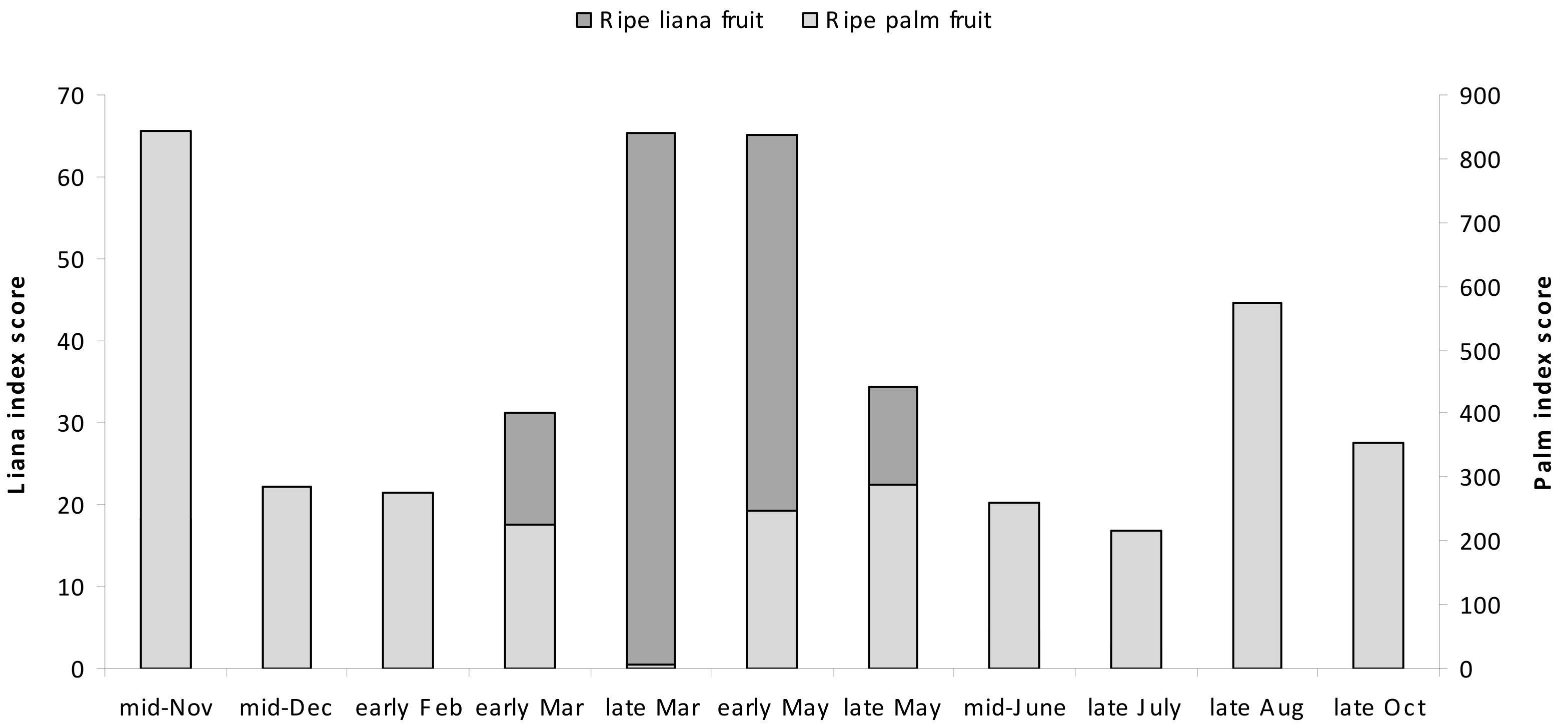

Figure 2.4. The availability of ripe liana fruit (10 species) and ripe palm fruit (4 species) at La Chonta, November 2003 to October 2004 (see methods for index score explanation).

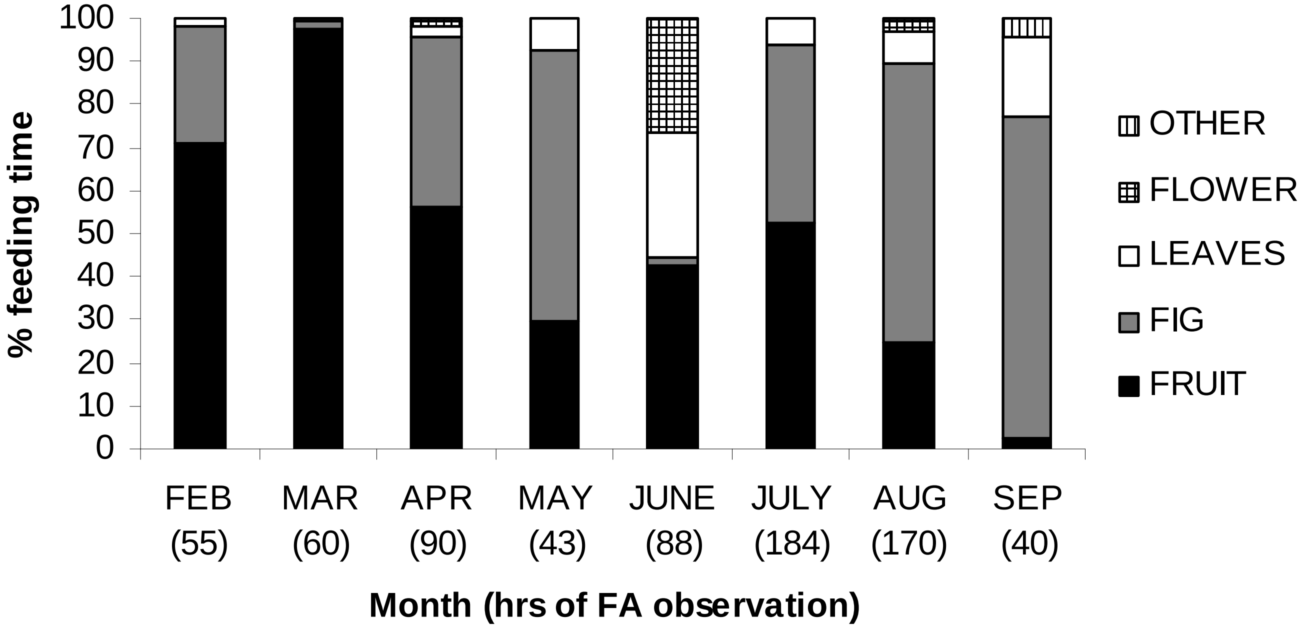

Figure 2.5. Monthly proportions of dietary items in feeding time budgets of focal follow animal (FA) of *Ateles chamek* in La Chonta.

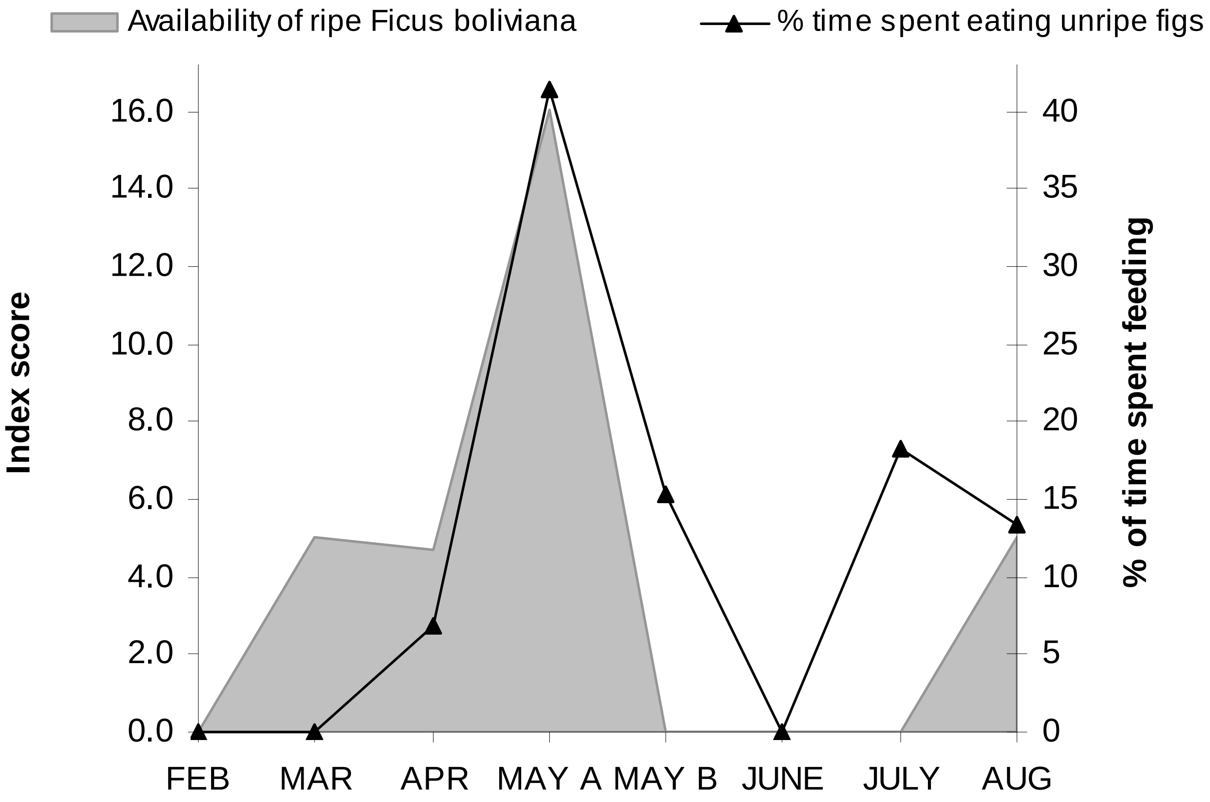

Figure 2.6. Percentage time spent feeding on unripe figs (88% of which was *Ficus boliviana*) and the availability of ripe *F. boliviana* in the home range. Two phenology surveys were conducted in May (A: early May, and B: mid-late May). Index score = % surveyed trees with ripe crops x basal area.

2.5. Discussion

By studying *Ateles chamek* in the forest of La Chonta we have discovered some new aspects of ateline biology. First, *Ficus* appears to be a staple food, not a fall-back food, for *Ateles chamek* in this forest. Second, *Ateles chamek* spend more time feeding on unripe fruit pulp than has previously been observed (Di Fiore et al. in press). Surprisingly, *Ficus* was the predominant source of unripe fruit, which were harvested despite the fact that ripe figs and other ripe fruits were available at the time. Throughout this discussion we compare our results with those obtained from studies of other members of the genus *Ateles*. This approach is justified by previous research which demonstrated that both intra- and inter-specific distinctions in ateline feeding ecology are best explained by differences in the local food resources, rather than taxonomic distinctions of the *Ateles* species being considered (Russo et al. 2005).

The observed dietary composition for *Ateles chamek* in this study generally concurs with previous findings on *Ateles* (Table 2.5). The proportion of fruit in their overall diet falls within the upper range of previous studies, as does the percentage of leaves. During the period of fruit scarcity, *Ateles chamek* consumed fruit from a small number of plant species, supplemented by young and mature leaves, and flowers. This observation also corresponds with several other studies (Table 2.5). *Myrciaria* sp. was a critical source of ripe fruit for *Ateles chamek* during periods of fruit scarcity, as this species provided crops when little else was available.

As reported for other atelines (e.g. Terborgh 1983; Cant 1990; Wallace 1998; Serio-Silva et al. 2002; Russo et al. 2005), Moraceae was the most important plant family in the diet of *Ateles chamek* in La Chonta, both in terms of number of species and time spent feeding. Three of the top five species in their diet belong to this family (*Ficus boliviana, F. trigona* and *Pseudolmedia laevis*). Besides Moraceae, 36 other plant families and 63 different species featured in their diet. Despite the breadth of plant species from which focal animals consumed items, their diet was strongly biased in terms of the proportion of time spent feeding on certain food sources. Just two species comprised almost 50% of their total time spent feeding. In contrast, 86% of the recorded food species were each represented by ≤1% of total feeding time.

Such heavy reliance on just a few plant species is a common pattern for *Ateles* communities (Chapman 1988; Cant 1990; Nunes 1998; Dew 2005; Wallace 2005).

Plant resources that feature strongly in an animal's diet are not necessarily preferred, as they may be selected in relation to their availability in the habitat. We found a great range in preference indices indicating that a few taxa were strongly preferred; a few were strongly avoided, while a large number of taxa were consumed according to their availability (Table 2.3). The most highly preferred species by *Ateles chamek* in La Chonta was *Virola sebifera* (Myristicaceae). This species is rare in the study area and we observed *Ateles chamek* to eat its fruit only on a few occasions. Trees of the genus *Virola* produce lipid-rich fruit that feature prominently in *Ateles* diets in several studies (van Roosmalen 1985; Stevenson et al. 2000; Dew 2005; Russo et al. 2005). *Ficus* was also highly ranked in our preference analysis, which mirrors the observed disproportionate consumption of fruit from this genus: 49% of all time spent feeding was spent in *Ficus*.

Ficus is one of the most widespread genera of tropical plants (Janzen 1979). The phenology of *Ficus* is unique, as fig trees depend on species-specific symbionts (agonid wasps) for their pollination and have evolved to produce very large crops of fruit at short intervals that favor the continuous development of these symbionts (Janzen 1979). It is this combination of large fruit crops and asynchronous intra-population fruiting that makes fig trees important resources for many tropical frugivores (Leighton & Leighton 1983; Terborgh 1983;1986; Shanahan *et al.* 2001). In addition, figs provide a range of essential nutrients and minerals (Conklin & Wrangham 1994; O'Brien, Kinnaird & Dierenfeld 1998). Despite all the mentioned benefits of *Ficus*, relatively few Neotropical frugivores actually seem to prefer figs when other fruit are highly available (Milton et al. 1982; Shanahan et al. 2001). Exceptions to this rule include fig-specialist fruit bats (e.g. August 1981), and some populations of predominantly folivorous howler monkeys that eat figs at all times of the year (*Allouatta palliata* in Panama: Milton 1980). Spider monkeys in La Chonta may have to be added to this list of exceptions.

Our results clearly show that figs were a preferred food both during times when ripe fruit was plentiful in their home range and when it was scarce. Such consistent consumption of *Ficus,* regardless of alternative food availability, has not been observed previously for spider monkeys, even though the use of *Ficus* has been reported in every single *Ateles* study to date (Di Fiore et al. in press). *Ficus* played a major role in the diet of *Ateles chamek* in six of the nine months of detailed feeding data collection (Table 2.4). In fact, in three months *Ficus* contributed to more than 40% of their feeding time budget. Statistically, the availability of figs was the driving factor behind daily time spent feeding. In contrast, the average dietary contribution of *Ficus* as reported for other *Ateles* study communities is 9% (range 0.9%-29%, Table 2.5. The contribution of *Ficus* does not appear to be related to the diversity of *Ficus* species included in diets (Table 2.5). The one study in which an *Ateles* community consumed figs at a proportion (29%) that was comparable to that seen in La Chonta, involved *A. geoffroyi* in Santa Rosa National Park, Costa Rica (Chapman 1987;1988). Heavy reliance on figs by both study communities may be related to the fact that both forests are semi-deciduous with marked seasonal differences in rainfall and temperature that results in longer-than-normal dry seasons (Janzen 1983; Justiniano & Fredericksen 2000). Why these aspects of forest ecology appear to coincide with higher dependence by *Ateles* on *Ficus* is as yet not understood.

The time *Ateles chamek* spent eating figs was almost equally divided between the two most commonly occurring species *Ficus boliviana* (50%) and *F. trigona* (48%). Interestingly, the two species were harvested for figs at different maturity phases: 65% of the time spent eating *Ficus boliviana* figs was on the consumption of unripe figs, while the equivalent value for *F. trigona* was only 10%. *Ficus boliviana* was the primary source of unripe fruit in general (68%). Unripe figs are normally not reported as a significant food item for *Ateles* (Table 2.5). Only in one publication did we find information on this food item and the author reported a proportion that was very small (0.1% of total feeding time, Wallace 1998). Some of our feeding observations of unripe figs occurred when ripe figs were scarce in the home range (Figure 2.6). Such periods of ripe fig scarcity were the result of synchronous fruiting pattern of the most common *Ficus* species in this forest. Periods of ripe fig scarcity may not be annual, or even of frequent occurrence in La Chonta. It is known that great inter-annual differences in *Ficus* phenology occur (Milton 1991), and *Ficus* elsewhere in La Chonta has been documented to provide ripe fruit crops continuously over the year (Fredericksen et al. 1999) . However, we have shown that at the scale of a spider monkey community's home range, critical periods of ripe fig scarcity do occur. During such times, unripe fig crops are available (Figure 2.3), because an individual tree's crop stays unripe for three to four times as long as it stays ripe (Norconk, Grafton & Conklin-Brittain 1998). Such difference in temporal availability would explain their choice of unripe figs during times of ripe fig scarcity.

Surprisingly, *Ateles chamek* also consumed unripe figs at times when ripe figs were abundant. Unripe figs of *Ficus boliviana* were consumed both at times when ripe figs from this species were plentiful, as well as when ripe fruit in general were highly abundant (Figure 2.6). Interestingly, a similar pattern was observed in a chimpanzee (*Pan troglodytes*) community in Uganda where 1) figs and leaves of *Ficus* were constant staple foods, featuring in their diet all through the year, and 2) several of the *Ficus* species were harvested for their unripe figs as well as the ripe, with the unripe figs occasionally preferred (Newton-Fisher 1999).

Ficus was not the sole provider of unripe fruit. Overall, *Ateles chamek* fed on unripe fruit for 23% of their feeding time. No other *Ateles* studies have documented as many months in which unripe fruit pulp make up >5% of feeding time (Table 2.5). The period with the highest percentage of unripe fruit consumption time was May (45%), a month which fell within the long period of fruit scarcity. Unripe fruit, often in combinations with leaves, is often reported as an important fall-back food for spider monkeys during lean times (Milton 1993a; Iwanaga & Ferrari 2001; Wallace 2005). Indeed, due to limitations of their gut morphology and digestive abilities, spider monkeys cannot switch entirely to folivorous diet in times of fruit scarcity (Milton 1993a), thereby potentially increasing their requirement for unripe fruit at these times. However, even during months with high recorded general food availability *Ateles chamek* spent a large amount of time eating unripe fruit and figs (July: 23% and August: 18%). In La Chonta unripe fruit is therefore an almost continuous component of their diet, rather than a back-up food resource consumed only in times of general food scarcity.

It is important to clarify the difference between unripe pulp consumption and the consumption of unripe fruit for the purpose of digesting the seeds. True seed predation is a rare phenomenon in the diets of *Ateles* (Di Fiore et al. in press). In their multi-site comparison of *Ateles* seed dispersal, Russo et al (2005) found that on average only 3.2% of feeding observations involved seed predation (range 1.1-6.5%). They describe seeds as predated if they are ingested but not defecated intact, or if they were masticated before ingestion. Besides spitting out the large seeds of palm fruit, *Ateles chamek* in La Chonta swallowed seeds of all fruit sources whole and passed seeds intact. They were never observed to masticate seeds. Even though seeds typically mature somewhat earlier than the pulp (Janson & Chapman 1999) we have no evidence as to whether seeds from unripe fruit and figs consumed by *Ateles chamek* in this study were viable or not. If they are not viable, the action of removing immature seeds from the tree, and thus prohibiting the seeds to mature, leads to similar seed fate as in cases of true seed predation. To understand the actual impact of such seed removal on tree regeneration, researchers need to test seed viability across a range of developmental stages of unripe fruit consumed by spider monkeys.

Inter-annual variation in spider monkey diet composition can be high (Chapman 1987), and admittedly our study is but a glimpse of time in the lives of this community. Given that our study period overlapped with both periods of fruit abundance and scarcity, and observed rainfall was similar to the annual averages for this forest, we make the assumption that our results are representative of this primate population's normal patterns. *Ficus* is regarded as an important resource due to the critical role of this genus in the ecology of tropical frugivores in times of fruit scarcity (Terborgh 1983;1986; Shanahan *et al.* 2001). The heavy reliance on *Ficus* in this study elevates the value of *Ficus* from a fall-back food, to an important food source throughout the year. Such a change in mind set, to regard figs as an all round important staple food, has been made for bonobos and chimpanzees (Wrangham et al. 1993; Conklin & Wrangham 1994; White 1998; Newton-Fisher 1999). We suggest that a similar change in appreciation of fig trees should be reached for Neotropical frugivores for which figs constitute a staple. This is important as free-standing fig trees like *Ficus boliviana* are harvested for timber. Bolivian forests such as La Chonta are becoming more and more deficient in young and mature individuals of this species (Mostacedo & Fredericksen 1999). It is of great conservation concern to understand in what way a decline in this staple food source will affect the *Ateles chamek* population.

2.6. Acknowledgements

This project was supported through the generous financial assistance of the Wildlife Conservation Society, Conservation International, the Rufford Foundation and the Primate Society of Great Britain. We thank the personnel of Instituto Boliviano de Investigación Forestal (IBIF), Agroindustría Forestal La Chonta Ltda, and el

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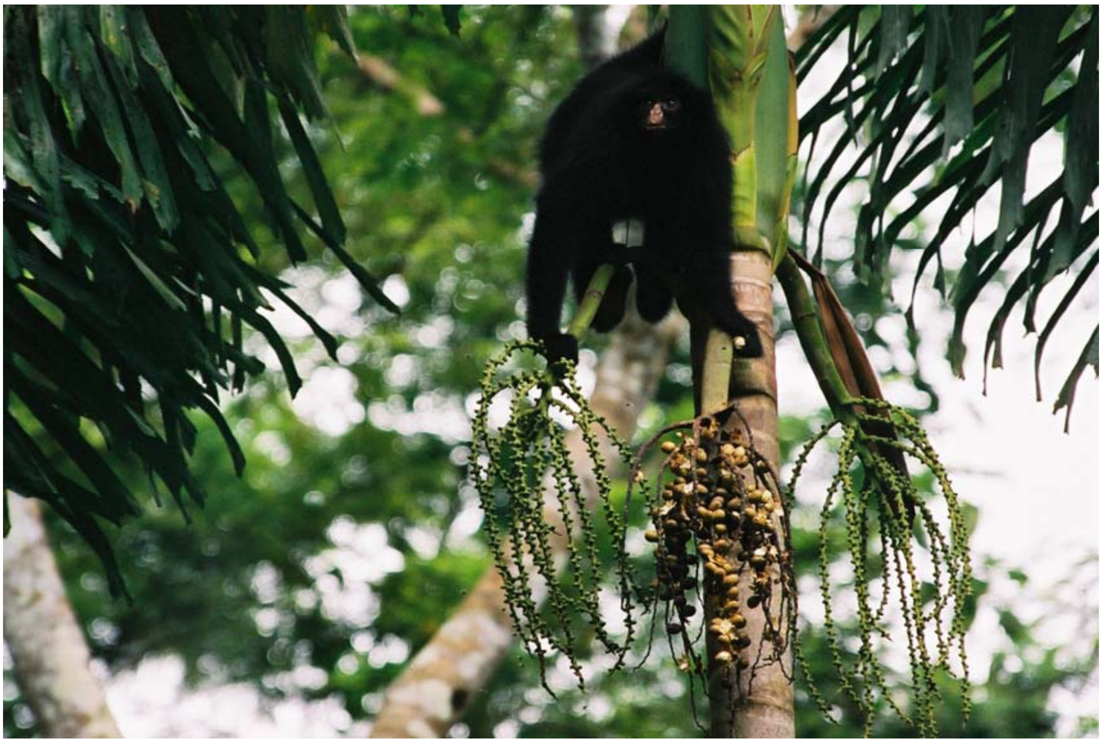

Photo by Renna Short

A male spider monkey visiting a palm tree (*Socratea exorrhiza*) which carries ripe and immature fruit

Chapter 3 – Nutritional regulation in wild spider monkeys: A possible link to human obesity

Citation: Felton, A.M., Felton, A., Raubenheimer, D., Simpson, S.J., Foley, W.J., Wood, J. Wallis, I.R, and Lindenmayer, D. B. (in review). Nutritional regulation in wild spider monkeys: A possible link to human obesity. Proceedings of the National Academy of Sciences of the United States of America.

3.1. Abstract

The modern obesity epidemic has been attributed to a mismatch between modern diets and phenotypes that evolved in Paleolithic nutritional ecologies. Understanding the nutritional strategies of free-living, non-human primates may offer new insights into the origins of human susceptibility to obesity. This information can also contribute to the effective management of wild and captive primate populations. However, relevant information is scarce as studies of the nutritional strategies of wild animals pose considerable practical challenges. Here we use recent advances in nutritional theory to analyse detailed data on food selection and nutrient intake by wild Peruvian spider monkeys (*Ateles chamek*). We show for the first time that nutrient balancing is the primary goal of diet selection in a non-human primate. Our analysis shows that alternative hypotheses traditionally used to explain vertebrate diet selection, such as energy or protein maximization, or avoidance of plant secondary metabolites, cannot explain the observed pattern of nutrient intake. Instead we show that protein intake by spider monkeys resembled that of humans: protein intake was regulated more tightly than either carbohydrates or fats, and disproportionately influenced total energy intake. These similarities between Homo and Ateles indicate that the origins of human susceptibility to obesity may date before the previously speculated Paleolithic era. Our results also provide a deeper understanding of primate nutritional ecology that is directly applicable to forest management and primate conservation.

3.2. Introduction

Understanding the nutritional strategies of non-human primates in the wild can provide insights into human nutritional ecology. For example, comparative analyses of the diets consumed by non-human primates have illuminated the origins of human meat-eating (Milton 1999) and micro-nutrient requirements (Milton 2003b). Insights gained from studying the nutritional ecology of wild animals are also relevant to conservation, as they enable us to determine which nutritional resources may be important for animals in captivity (Agoramoorthy, Alagappasamy & Hsu 2004; Lambert 2007), and for animals whose habitat has been disturbed by humans (Raubenheimer & Simpson 2006; Rode *et al.* 2006).

There are four major schools of thought in nutritional ecology, each of which proposes that diet selection subserves a different primary nutritional goal: (i) energy maximization (Schoener 1971); (ii) nitrogen maximization (Mattson 1980; White 1993); (iii) regulation of plant secondary metabolites (Freeland & Janzen 1974; Dearing *et al.* 2005) and (iv) nutrient balancing (Raubenheimer & Simpson 2004; Robbins *et al.* 2007). Quantifying the relative influence of these different nutritional goals is challenging, especially in studies of wild animals. Research of this nature requires detailed data on feeding behaviour from individual animals over continuous periods, relevant analyses of all foods consumed, and an analytical framework for dealing with the complex, multivariate nature of nutritional data. Here, we apply recent advances in nutritional theory to a uniquely detailed field data-set and demonstrate the nutritional goals of Peruvian spider monkeys (*Ateles chamek* Humboldt 1812, subfamily Atelinae) inhabiting an undisturbed semi-deciduous forest in lowland Bolivia.

Energy is often proposed to be the primary driver behind atelines' diet selection (Rosenberger & Strier 1989; Strier 1992; Di Fiore & Rodman 2001). This is because ateline primates are frequently observed to preferentially select and consume large volumes of fruit that are rich in lipids and soluble carbohydrates (Castellanos 1995; Dew 2005; Di Fiore *et al.* in press). In order to assess the nutritional underpinnings of spider monkey diet selection, we observed the feeding behaviour of 15 focal animals continuously from dawn to dusk. We collected samples of their food, and analysed the nutritional composition and the presence of certain plant secondary metabolites. The macro-nutrient content of diets (we include carbohydrates, lipids and protein in the term ‘macro-nutrients’) differed widely during the nine month study period, and the relative abundance of different food types varied markedly between seasons. These sources of variation allowed us to address the extent to which energy, protein, and non-nutrient chemicals determined patterns of intake. Data were analysed using the Geometric Framework, a multidimensional approach designed to assess the relative priorities assigned by animals to different food components (Simpson & Raubenheimer 1993) (Fig. 3.1a).

3.3. Results and Discussion

Our results (Fig. 3.1b) fit the prediction of the protein leverage hypothesis (line *p* in Fig. 3.1a): intake of daily available protein (hereafter referred to as "protein", P, see Methods for details on digestibility assay) was regulated more tightly than either carbohydrates or fats, and disproportionately influenced total energy intake. The protein leverage hypothesis predicts that in the most extreme case, non-protein energy intake (i.e. intake of non-structural carbohydrates plus lipids; C+L) will decrease hyperbolically with an increasing proportion of protein in the diet, whereas protein gain will remain constant (Simpson & Raubenheimer 2005). The observed macro-nutritional intake by spider monkeys closely resembled the pattern expected by this model (Fig. 3.2). Monkeys maintained their daily intake of available protein at a mean of 0.19 MJ (± 0.01 SE), whereas non-protein energy varied between 0.7-6.2 MJ (mean 1.82 MJ ± 0.82 SE; Fig. 3.1b, Fig. 3.2). The variation in daily intake of non-protein energy was significantly related to the availability of ripe fruit in the spider monkey territory (Supporting Information (SI) Table 3.2).

Neither energy nor protein maximization alone could account for the observed pattern of feeding, contrasting previous suggestions that energy is the primary driver behind food choice in frugivorous atelines (Strier 1992; Di Fiore & Rodman 2001). Daily nutrient intake trajectories did not conform to either the most energy-rich or the most protein-rich foods that were abundant in the environment (Fig. 3.3). Furthermore, protein intake was not related to the percentage of non-fruit items in the diet (i.e. leaves and flowers: $R^2 = 0.004$, $p = 0.719$), nor to temporal fluctuations in the abundance of different food items throughout the field study (SI Table 3.2) which spanned distinct periods of abundance and scarcity of different food resources (Felton *et al.* 2008b). This indicates that individuals reached their protein target regardless of which food choices were available. To maintain a stable intake of protein, spider monkeys consumed large amounts of C and L when protein content in the food was low, e.g. when their diet consisted entirely of ripe fruit.

Plant secondary metabolites (PSMs) may have played a role in determining which foods spider monkeys chose to eat and which to reject. However, on the scale of nutrient intake gained from selected foods, our results demonstrate that PSMs did not dominate the patterns observed. Tannins greatly reduce the availability of protein (Robbins *et al.* 1987), and occur to a great extent in both leaves and fruit consumed by spider monkeys (leaves, mean 12% ± 0.55 SE; fruit, mean 10% ± 1.33 SE; tannin concentration measured as % bound polyethylene glycol). There was no relationship between dietary tannin and intake of protein ($R^2 = 0.014$, $p = 0.473$) or non-protein energy sources ($R^2 = 0.000$, $p = 0.994$). However, the data suggest that C+L intake was reduced when tannin levels were higher than 16% by dry mass and protein levels in the diet were also low (Fig. 3.4). This finding is in keeping with other research showing that tannins have a disproportionate impact on food intake when protein levels in food are low (Simpson & Raubenheimer 2001; Villalba & Provenza 2005).

When explaining feeding patterns of animals, some branches of nutritional ecology (e.g. optimal foraging theory, Schoener 1971) emphasize constraining factors such as gut limitations and time spent feeding (Mattson 1980). These constraints cannot explain our results. Focal animals were observed to consume up to 2.4 kg fresh matter per day but averaged only 1.0 kg/day (SE 0.08 kg), which indicates that volumetric constraints could not explain the data. Nor was there a relationship between total food and fiber intake ($R^2 = 0.007$ $p = 0.620$). Daily feeding time varied between 52 – 400 min (mean 173 ± 12.5 SE), and there was no relationship between daily feeding time and protein intake ($R^2 = 0.039$, $p = 0.209$) or C+L intake ($R^2 = 0.047$, $p = 0.167$). Finally, it is highly unlikely that an upper limit to protein intake limited total energy intake. This is because toxic effects of over-consumption are noticeable only when animals ingest amino acids at much higher amounts than those encountered in our study (Harper, Beneveng.Nj & Wohlhuet.Rm 1970; DeGabriel, Foley & Wallis 2002).

Our results demonstrate that nutrient balancing best describes the nutritional strategy of these spider monkeys, and while their daily protein gain is comparatively low, the amount of protein ingested daily is maintained remarkably stable despite significant variation in food composition. Such findings can contribute to the management of wild populations, by characterizing conservation problems in terms of nutrient landscapes. For instance, figs of the commercial timber species *Ficus boliviana*[1] were a major food source for our study animals (Felton *et al.* 2008b), and also appear to be a nutritionally-balanced food for spider monkeys (Fig. 3.3). Nutritionally-balanced food sources that are used extensively by a wild population may need special attention in conservation planning, e.g. as the basis for exempting certain tree species from logging, or as target tree species for establishment in vegetation restoration. A more complex picture also emerges from our analysis, in which the monkeys are able to regulate their nutritional state through selecting complementary combinations of other foods. A challenge therefore is to conserve a diversity of foods which provide foragers with access to the optimal region within nutrient space (Fig. 3.1a).

Our findings are of interest in understanding the evolutionary and ecological origins of human susceptibility to obesity. Human obesity and associated disease is commonly attributed to a mismatch between modern diets rich in carbohydrates and lipids, and phenotypes that evolved in Paleolithic nutritional ecologies where diets were relatively high in protein and fiber (Eaton, Eaton & Konner 1999; Cordain *et al.* 2000). Given the evidence that the regulatory dominance of protein over non-protein energy plays a central role in human obesity (Simpson & Raubenheimer 2005), the existence of a similar regulatory pattern in a frugivorous platyrrhine primate suggests that the genetic origins of human susceptibility to obesity could be far older than the Paleolithic. This is consistent with the hypothesis that human micro-nutrient requirements have a pre-Paleolithic origin (Milton 2003b). Anatomical, physiological and paleontological evidence support the general consensus that the ancestral form giving rise to the human (*Homo*) lineage was markedly herbivorous, similar to modern apes and monkeys (Milton 2000;2003b). Furthermore, the extensive homology of the "obesity gene product" among vertebrates also suggests that susceptibility to obesity may have ancient origins (Zhang *et al.* 1995). We hypothesize that although the gut morphology of *Homo* has evolved to digest higher quality food compared to apes and monkeys (Milton 2003a), the mechanisms for

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[1]. The taxonomy of this species is uncertain at the time of printing. This species may be *Ficus insipida* (synonym *F. glabrata*), but because the name *F. boliviana* is the accepted classification employed by Bolivian researchers I have chosen to use it throughout the thesis. Please contact the author for updated nomenclature.

macro-nutrient regulation have remained relatively unchanged. We recommend that further comparative studies into nutritional strategies of wild non-human primates, representing a wide range of diets and phylogenetic relatedness to humans, are conducted to elucidate this issue. The findings of this study also suggest that an adjustment of the macro-nutritional balance of diets as a means to manage human obesity might similarly be an option for mitigating the common problem of obesity in captive primates (Terranova & Coffman 1997; Videan, Fritz & Murphy 2007).

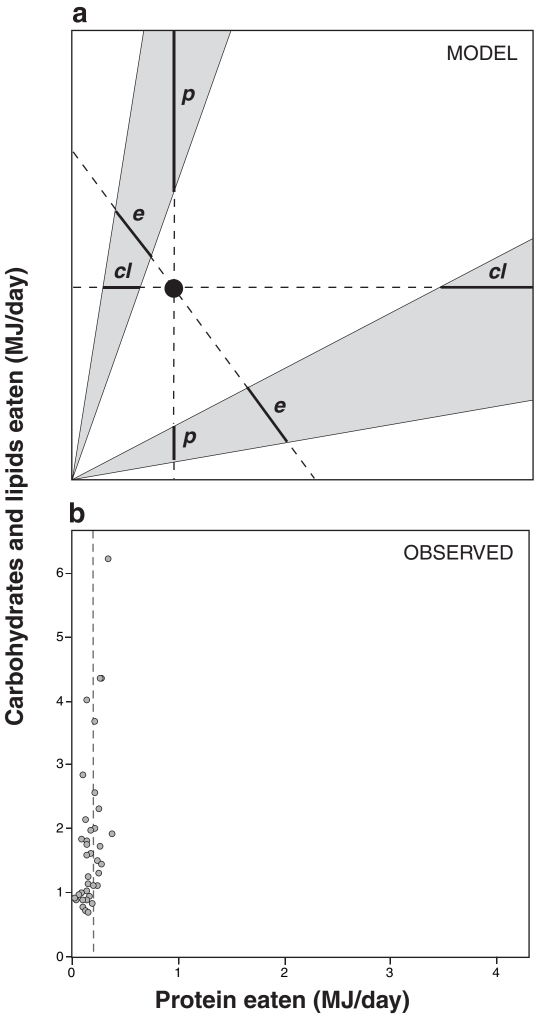

Figure 3.1. Predicted and observed outcomes of diet selection. (a) A model using the Geometric Framework to represent potential outcomes when animals are fed diets containing different ratios of protein (P) versus carbohydrates (C) and lipids (L) (Simpson, Batley & Raubenheimer 2003). When animals are free to choose foods representing the entire spectrum of P:(C+L) ratios, two outcomes are plausible: (i) daily nutritional intakes fall along line e due to energy maximization subject to constraints, or (ii) daily intakes converge around a point in nutritional space (dot) due to target regulation through nutrient balancing. Lines emanating from the origin represent "food rails" which indicate the food's ratio of P:(C+L). When animals are restricted to diets containing limited amounts of either P or C+L (shading), three outcomes are plausible: (i) total energy intake is prioritized (intake points fall along line segments e); (ii) C+L intake is prioritized (segments cl) or (iii) protein intake is prioritized (segments p). (b) Each point represents the daily endpoint in nutritional space of a focal animal in this study (38 daily follows). The vertical line, which represents mean protein intake, fits protein prioritization in Fig. 3.1a. Protein intake data indicate available protein and account for any protein bound by tannins (see Methods). There were no significant differences in macro-nutrient intake between sexes or individuals (SI).

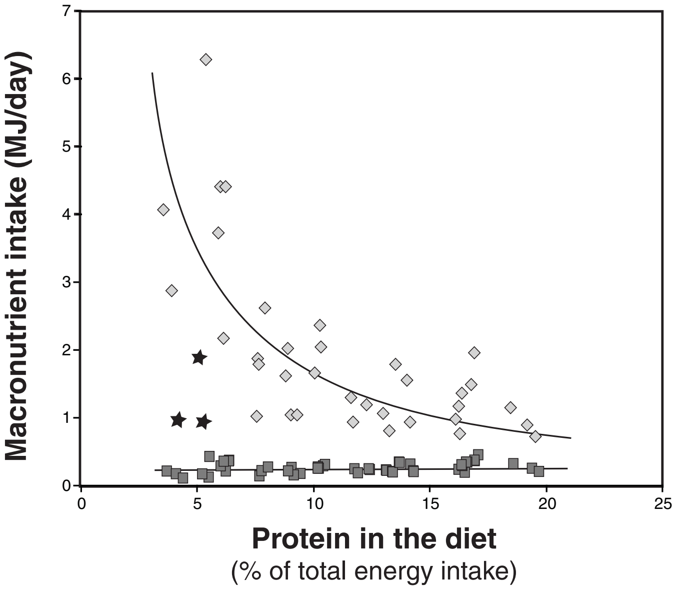

Figure 3.2. Macro-nutrient intake across varying diets. Relationship between observed intake of protein (squares) and non-protein energy (C+L, diamonds) across a range of diets with varying proportions of protein, in relation to the expected C+L intake (hyperbolic trend line) assuming complete protein leverage (i.e. intake of protein is maintained constant when diet composition varies). We used data from 38 focal days to calculate the expected C+L intake according to the equation $C+L = (P_t/p) - P_t$; where P_t is the target intake of protein and p is the proportion of protein of total energy intake (Simpson et al. 2003). We assumed that the observed mean protein intake approximated the physiological target intake P_t. Absolute protein intake did not vary across diets ($R^2 = 0.034$, $p = 0.287$, horizontal trend line). Stars indicate days when dietary tannin was exceptionally high and likely caused C+L intake to be lower than expected (see Figure 3.4 and SI). C+L intake varied significantly across diets including or excluding days with high dietary tannins (*n* = 38, $R^2 = 0.313$, $p < 0.001$; *n* = 35, $R^2 = 0.452$, $p < 0.001$).

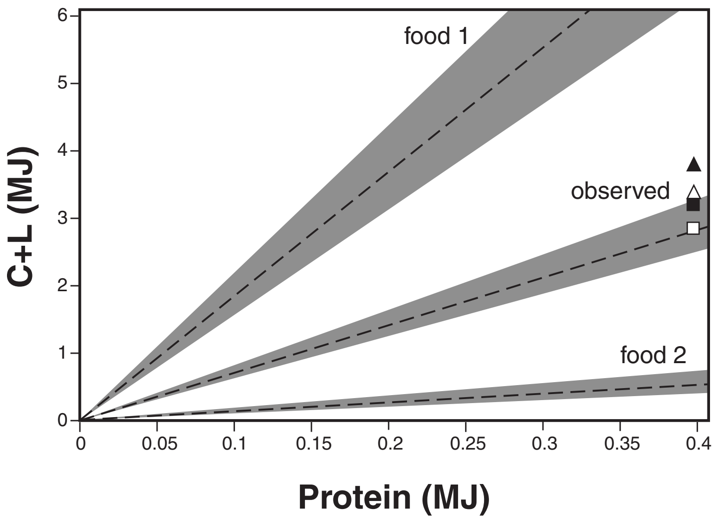

Figure 3.3. Observed intake versus macro-nutrient balance of food groups. Comparison of the mean observed intake trajectory across all observation days (“observed”) with food rails representing the mean of the lowest (“food 1”) and the mean of the highest P:(C+L) foods (“food 2”) that were sampled by the monkeys on each day and were abundant in the home range (shaded areas = 95% confident intervals). The three means were significantly different from each other ($p < 0.001$). The low P:(C+L) food group had significantly higher total energy content ($p < 0.001$) and lower protein content ($p < 0.001$) than the high P:(C+L) food group. Also indicated are the positions of four species of ripe fruit that appear to have balanced macro-nutritional compositions in relation to the animals’ average intake trajectory (▲: *Ficus boliviana*; △: *Socratea exorrhiza*; ■: *Jacaratia spinosa*; □: *Celtis iguanea*). The observed intake was not a product of individuals consuming large quantities of *Ficus boliviana*, their staple food (Chapter 2). The intake trajectory of days when figs were absent from their diet was not significantly different from the overall mean ($n = 12$, $p = 0.155$). This supports the conclusion that *Ficus boliviana* and other foods indicated in the figure are indeed nutritionally-balanced foods for these primates.

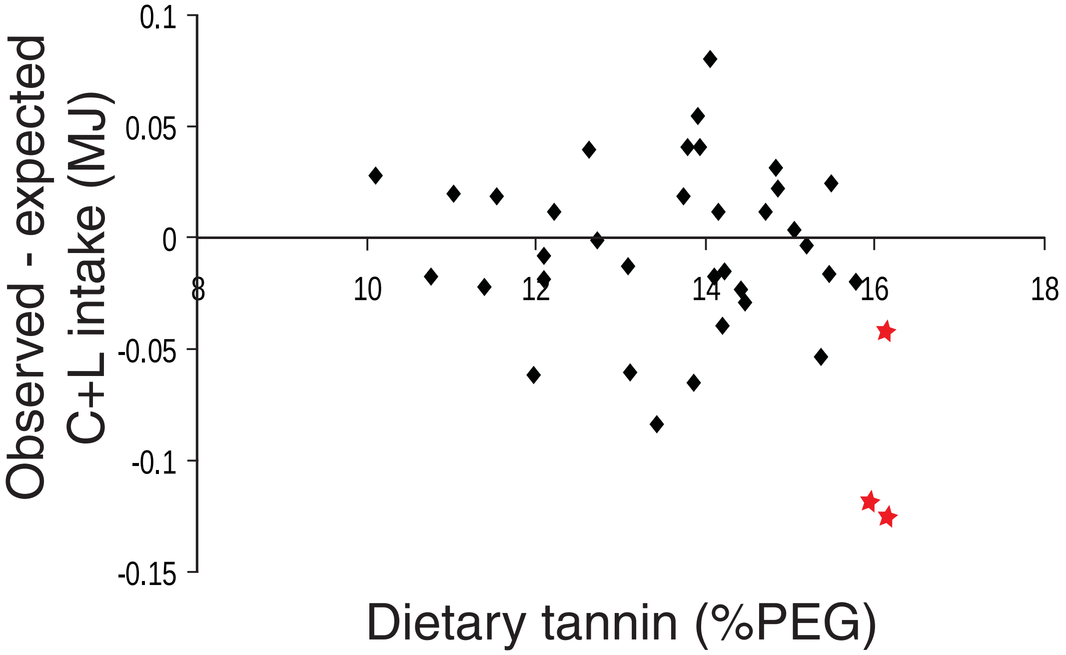

Figure 3.4. The perpendicular distance between the observed and expected C+L intakes for each day (which are both depicted in Figure 3.2) in relation to tannin content in the corresponding diet. Tannin concentration was measured as % bound polyethylene glycol (PEG). All three data points that fall above 16% PEG (denoted as stars in this figure and Figure 3.2) deviate significantly more from the expected C+L intake than the remaining points ($p < 0.001$) and represent days when protein constituted ≤5% of total energy intake.

3.4. Materials and Methods

3.4.1. Study site and field methods

A.M. Felton collected data in the lowland semi-deciduous moist forest of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. The study area (S: 15° 36’ 26.3 to 15° 37’ 44.5 and W: 62° 46’ 58.9 to 62° 47’ 55.7) was located in an undisturbed section of the 100,000 hectare forestry concession “La Chonta”, which is owned and managed by Agroindustría Forestal La Chonta Ltda. Average annual precipitation for La Chonta is 1570 mm and average annual temperature is 25°C. The seasonal distribution of rainfall during the study was representative of the average monthly rainfall for the forest (Felton *et al.* 2008b). Previous research has shown that three distinct phenological periods were detectable in this forest during the course of this field study, including an initial period of high ripe fruit abundance followed by a ten week long period of fruit scarcity before ripe fruit became more abundant again (Felton *et al.* 2008b).

We established a network of trails in the study animals’ home range, which covered an area of 360 – 400 ha. We used this network for daily follows of focal animals, a vegetation survey and monthly phenology surveys. We collected basal area information from all trees over 10 cm DBH within 71 0.1 ha plots distributed throughout the community’s territory. Basal area information was used in calculations of relative availability of different food species in this forest.

For every month we calculated an index (T) of food availability originating from approximately 2000 trees:

$$\text{Index T} = \sum_i (p_i \times BA_i)*100$$

where p_i is the proportion of surveyed individuals of species *i* that carry an edible pheno-phase at a given time, and BA_i is basal area/ha of species *i*. We also broke down Index T into different categories: ripe fruit, unripe fruit, ripe figs, unripe figs and flowers. A detailed description of the design and sampling effort of our phenology surveys can be found elsewhere (Felton *et al.* 2008b).

We spent five months habituating the study community. Following habituation, we systematically collected feeding data from February 2004 to September 2004. We conducted continuous observations of the same focal individual from dawn to dusk, because the unit of interest for this study was the food intake per individual per day. Focal animals (FAs) were adults that were readily identifiable by facial and bodily markings. Females were lactating or pregnant, and caring for a dependent juvenile. We followed each FA for at least one whole day each month and alternated between male and female FAs on a daily basis. In this analysis we only include days where (i) the focal animal was successfully followed all day; (ii) all feeding events were documented in detail, and (iii) relevant analyses existed for every food item consumed. Using these strict criteria we included 38 follow days in the present analysis representing 7 males and 8 females. Male and female spider monkeys are of similar body weight (7.5-9kg) (Smith & Jungers 1997; Karesh *et al.* 1998). Individuals included in the analysis all appeared healthy (visual assessment in combination with results from urine test strips that were used opportunistically). Four focal animals gave birth to healthy offspring during the year of study.

We collected data continuously on the FA's activities. We noted the exact start and end time of each feeding event, including even very brief feeding events. We recorded the type of food item eaten, and took detailed notes on which parts of the fruit were consumed. We used differences in fruit size, color and consistency to differentiate between immature and ripe fruits. During each feeding event we noted the number of seconds the FA took breaks from ingesting food. Such breaks were subtracted from the feeding time to estimate the "ingestion time". We measured feeding rates (number of items ingested/ minute) opportunistically, using a stopwatch, when the FA or other individuals were in clear view and were eating continuously without taking a break.

We identified and tagged all plants that either the FA or other members of the subgroup were eating from. We collected food items from trees marked as feed trees, using tree pruners and tree climbing equipment. The collection took place one or two days immediately after the monkeys were observed to use the trees. Whenever possible we collected items from multiple feed trees of the same species, thereby incorporating between-tree and between-season variation in nutritional content (Chapman *et al.* 2003; Worman & Chapman 2005). If the monkeys were observed to eat only part of the fruit, we separated the components accordingly before drying (pulp, husk/ wall and seed). We kept samples in a drying oven (temperature maintained between 40-50ºC) until the dry weight maintained a stable minimum for several hours. We then packaged samples with silica desiccant. We transported samples to a cool and dry place, where desiccant was replaced.

3.4.2. Laboratory methods

We used near infrared reflectance spectroscopy (NIRS) (Foley *et al.* 1998) to estimate the concentrations of total nitrogen, lipid, starch, neutral detergent fiber, ash, PEG binding capacity, and *in vitro* digestible N in all food items. We could not obtain acceptable calibrations to estimate water-soluble carbohydrates (WSC) with NIRS and therefore used directly assayed chemical values for this measure. We used standard procedures for NIRS analysis (ANON 1995) using a FOSS 6500 spectrophotometer. We selected a representative subset of samples for the calibration data set and analyzed these sub-samples chemically. We carried out all chemical assays in duplicate. We used the Kjeldahl procedure for assaying total N, and petroleum spirit extraction in a Soxhlet apparatus for total lipid. We analyzed WSC and starch using the anthrone reaction and a Megazyme Total Starch kit respectively as described elsewhere (Lawler *et al.* 2006). Starch and WSC values were summed and presented as total non-structural carbohydrates (which in this paper is referred to as “carbohydrates” or “C”). We measured neutral detergent fiber (NDF) on the residue from lipid analyses using the ANKOM filter bag method (Van Soest, Robertson & Lewis 1991; Komarek 1994). Tannins were assayed as the amount of polyethylene glycol (PEG) bound per unit dry matter, and we estimated the effect of tannins on nitrogen availability using the *in vitro* digestion procedure described by De Gabriel and others (De Gabriel *et al.* in press). We thus estimated available protein as (total N x *in vitro* N digestibility) x 6.25 (in this paper referred to as “protein” or “P”). For the purpose of the geometric analysis we calculated the energetic value of the above nutrient fractions assuming the conventional conversion values of 37.7 kJ per g lipid, 16.7 kJ per g crude protein and 16.7 kJ per g non-structural carbohydrate (N.R.C. 1989).

3.4.3. Data analysis

When the absolute number of ingested items was not recorded for an event, we multiplied the ingestion time (see above) with the feeding rate that most closely matched the corresponding event. When available, we used the feeding rate of food item *i* (FR_i) recorded for the FA in question that particular event or day. In other cases we matched the event with alternative mean feeding rates in decreasing priority: an individual-specific mean FR_i; a sex-specific mean FR_i; or, in the last instance, a population mean FR_i. We multiplied the nutrient content per food item (g) by the estimated number of items ingested at each event, to obtain a total amount of each nutrient gained from each type of item. In this calculation we included nutritional data for the specific fraction or combination of fractions of each item that was consumed for each respective event (e.g. pulp only, 50% of fruit wall etc). We summed all daily events to obtain the observed daily nutrient intake ("OBS").

To test whether our macro-nutrient intake data conformed to the model predicted by the protein leverage hypothesis, we calculated the expected C+L intake by using the following formula (Simpson & Raubenheimer 2005):

$$C+L = (P_t/p) - P_t$$

where P_t is the target intake of protein and p is the proportion of protein of total energy intake. We assumed that the observed mean protein intake (0.19 MJ) approximated the physiological target intake (P_t in the equation). We also measured the perpendicular distance (*d*) from the observed to the expected C+L intake and contrasted *d* with the percentage of dietary tannin in the corresponding daily diets.

For each follow day we determined which was the lowest P:(C+L) food ("LOW") and the highest P:(C+L) food ("HIGH") that was available in abundance in the habitat (i.e. in the observer's judgment that food was sufficiently abundant to provide the focal animal with its full daily intake).

We used one-way analysis of variance (ANOVA) to test differences in protein and non-protein energy intake between individual focal animals. Two-way ANOVA was used to determine if there was a significant difference between the ratios P:(C+L) of the following three groups ($n = 38$ for each): LOW foods, HIGH foods (see above) and the observed daily intake of monkeys (OBS). To analyze whether the ratio P:(C+L) could be used as an indication of absolute amounts of total energy or protein in the food, we used one-way ANOVA to test whether the LOW and HIGH food groups were different in terms of total energy and protein content. We also assessed whether OBS was purely a product of the dominance of figs in their diet (45% of feeding time[24]) or whether the nutrient intake of individuals was similar regardless of the presence of figs. For this purpose we used one-way ANOVA to test whether OBS (n = 38) was different from the observed daily intake ratio of days when figs were not consumed at all (n = 12). We also used one-way ANOVA to test whether the perpendicular distance between observed and expected C+L intake (d, see above) was different for days with dietary tannins above or below 16% PEG.

We used principal component regression to assess the overall influence of food availability on nutritional composition of diets. In this data set, 13 out of the 38 follow days were excluded because we did not have closely matching phenology results (i.e. phenology survey was conducted less than 7 days before or after feeding observations were made). We first conducted a principal component analysis (PCA) using estimated daily intake (g) of ash, protein, carbohydrates, lipids, and NDF. To narrow down which indices of food availability were related to nutrient intakes, we used the resulting principal components as responses in a regression analysis (PCR) with the following indices as candidate variables: availability of ripe figs, unripe figs, ripe non-fig fruit, unripe non-fig fruit, and flowers. We selected regression models by considering all possible subsets of predictors and then choosing the model with the smallest value for the Akaike Information Criteria (Akaike 1974). To assess relationships between intakes of individual nutrients and food availability we used a similar regression model as above but limiting the availability indices to those found to be influential for the overall diet. We also used the same PCR procedure to assess whether there was a difference between sexes in terms of overall daily nutrient intake (principal components from the PCA).

We used an all-subsets linear model, with the same selection criteria as outlined above, to analyze the relationship between daily intake of available protein (MJ) and the following variables that varied on a daily basis: daily feeding time, dietary tannins (%PEG), % non-fruit items (leaves and flowers) in the daily diet, % protein in daily diet (P:(C+L)), and daily ash intake (g). The same candidate variables were also tested against daily intake of crude protein (total N x 6.25). We used simple linear regression analysis to analyze the relationships between fiber (NDF) intake and total food intake (fresh weight). We assessed the correlation between ash and protein content in food items using a simple correlation matrix.

To investigate the possible effect of between-animal variation we refitted our linear models as mixed models (McCulloch & Searle 2001). The between-animal component was negligible and non-significant and is ignored in the analysis reported here. The alpha-level was 0.05 for all statistical tests described above.

We applied the geometric framework as described in (Simpson & Raubenheimer 1995; Raubenheimer & Simpson 1997). The main sources of non-nitrogenous energy are carbohydrates and lipids, with lipids being approximately twice as energy-dense as carbohydrates. Lipids comprised only 13.8% of non-protein energy intake, and 12.5% of total energy intake. When plotted separately against protein intake, C and L contributed similarly to the non-protein energy curve. For the purpose of this analysis C and L can thus be regarded as interchangeable energy sources (Ruohonen, Simpson & Raubenheimer 2007). We therefore combined C and L into one axis (non-protein energy). For uniformity, protein was plotted in energy units. We acknowledge that the role of protein as an energy source to primates is minor but is predominantly used for growth and replacement of body tissue (Milton 1999; Leonard 2000).

3.5. Acknowledgements

We thank the Wildlife Conservation Society, Conservation International, the Rufford Foundation and the Primate Society of Great Britain for funding. Instituto Boliviano de Investigación Forestal (IBIF), Agroindustría Forestal La Chonta Ltda, and el Proyecto de Manejo Forestal Sostenible (BOLFOR) provided logistical support. M. Peña -Claros, T. Fredericksen, J. Justiniano, R. Wallace and C. Groves provided advice. J. Chuviña, G. Chuviña, R. Short, H. Peters and other volunteers provided assistance in the field. C. Hilliker helped with graphics. R. Heinsohn, M. Jennions, C. Groves and W. Steffen made comments on the manuscript.

3.6. Supporting Information

3.6.1. Supplementary Tables

Table 3.1. Statistical results from Principal Component Analysis of daily nutrient intakes of focal animals.

Variable (g)	PC1	PC2
Available protein (P)	-0.50	0.24
Non-structural carbohydrates (C)	-0.02	0.93
Lipids (L)	-0.46	-0.05
Ash	-0.52	0.05
Fiber (NDF)	-0.52	-0.26

Table 3.2. Results from all-subsets regression analysis of daily nutrient intakes versus the availability of ripe fruit and unripe figs, measures of food availability found to best explain the variation in nutritional composition of diets. Values represent coefficients of variation ± standard errors.

Daily intake (g/day)	Ripe non-fig fruit	Unripe figs	R^2
Available protein (P)	n.s.	n.s.	
Non-structural carbohydrates (C)	3.38 ± 0.57 ***	-1.59 ± 0.29 ***	0.62
Lipids (L)	0.13 ± 0.05 *		0.15
Ash		n.s.	
Fiber (NDF)	n.s.	n.s.	

Results are provided for the terms included in the regression model with the best AIC score.
* $p < 0.05$, *** $p < 0.001$

3.6.2. Supporting interpretation of results

Food items consumed by *Ateles chamek* ranged between 0.9-28% P, 1.8- 72% C and 0-75% L (all % of dry matter). There was no significant difference between sexes in daily nutritional intake either in terms of amount or composition (PC1: $R^2 = 0.004$, $p = 0.857$; PC2: $R^2 = 0.007$, $p = 0.562$; for explanation of PC1 and PC2 see below). Furthermore, there was no significant difference in macro-nutritional intake between individual focal animals (P: $p=0.843$; C + L: $p=0.945$).

3.6.2.1. Relationships between daily protein intake and factors that varied on a daily basis

We investigated whether factors other than protein regulation via nutrient balancing can explain the observed pattern in protein intake. Therefore, we assessed the relationship between protein intake and factors that varied on a daily basis. Daily intake of available protein was significantly related to only one of the five variables included in the regression model, namely ash (best regression model included 2 terms: $R^2 = 0.64$, ash intake $p < 0.000$, %PEG $p = 0.092$). This model included two variables that are hypothesized constraints to food intake, namely feeding time and amount of tannins in the diet (%PEG). Neither of these two variables was significantly related to crude protein intake (best regression model included two terms: $R^2 = 0.65$, ash intake $p < 0.001$, % non-fruit items in diet $p = 0.036$). Because neither feeding time nor dietary tannins negatively influenced protein intake, either total or digestible protein, we conclude that these proposed constraints do not explain the observed pattern of protein intake. The result from the above model also shows that absolute protein intake did not vary across diets that were characterized by a varying *proportion* of protein (as indicated in Figure 3.2), which instead can be explained by great variation in C+L intake.

Because ash (crude mineral) and protein concentrations were moderately correlated in food items ($r = 0.56$, $p < 0.001$), mineral intake by our focal animals was correspondingly related to protein intake (see results from model above). This relationship raises the interesting possibility that the intake of protein and minerals are mechanistically linked, but more data are needed to test this.

3.6.2.2. Relationship between macro-nutrient intake and monthly variation in food abundance

Two principal components explain the diet of focal animals (Table 3.1). The first principal component (PC1, explaining 61% of variation) describes the average amount of nutrients consumed. The second principal component (PC2, explaining 22% of variation) describes the nutritional composition of the daily diets, and is therefore more relevant in the current analysis. PC2 was significantly related to two indices of food availability ($R^2 = 0.50$): unripe figs ($p < 0.001$) and ripe, non-fig fruit ($p < 0.001$). These two indices were, in turn, most strongly related to the daily intake of C, while protein intake was not significantly related to either of the two indices (Table 3.2). These results lend further support to our conclusion that in contrast to C and L, monkeys maintained protein intake relatively constant throughout the study, despite variation in food availability in the habitat.

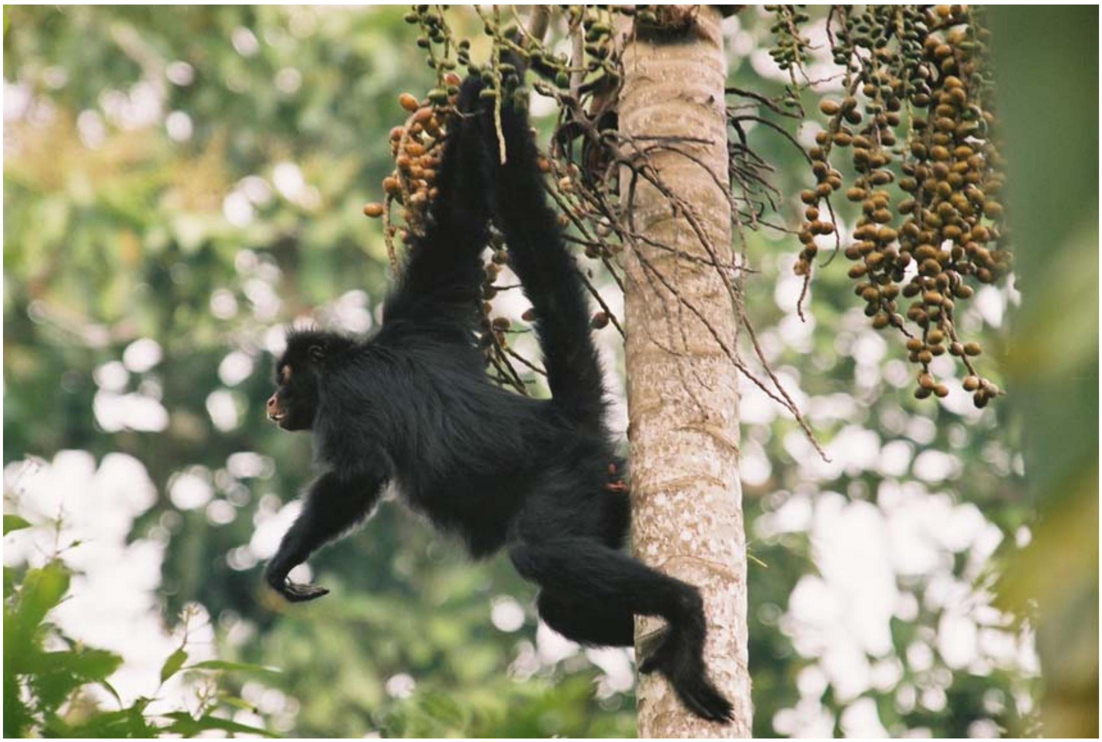

Photo by Renna Short

A female spider monkey feeds in the palm tree *Socratea exorrhiza*.

Chapter 4 – Nutritional ecology of spider monkeys (*Ateles chamek*) in lowland Bolivia: How macro-nutrient balancing influences food choices

*Citation: Felton A.M., Felton, A., Foley, W.J., Raubenheimer, D.,Wallis, I.R, Wood, J.T. and Lindenmayer, D. B. Nutritional ecology of spider monkeys (*Ateles chamek*) in lowland Bolivia: How macro-nutrient balancing influences food choices. To be submitted to* American Journal of Primatology.

4.1. Abstract

Research shows that diet selection by spider monkeys (*Ateles chamek*) is governed by protein-dominated macro-nutrient balancing. Here we assess the influence of this nutritional strategy on daily and seasonal nutritional intakes, estimate the nutritional value of different foods, and interpret unusual food choices. We conducted continuous all-day observations of focal spider monkeys inhabiting a semi-deciduous moist forest in Bolivia. We recorded feeding events, collected foods and analyzed their nutrient content. By using the Geometric Framework for nutrition, we show that individuals reached their daily end-point in nutrient space (balance between protein and non-protein energy intake) by consuming nutritionally-balanced foods or by alternating between nutritionally complementary foods. The seasonal availability of foods dictated the strategy and the resultant nutritional state of individuals. The macro-nutritionally balanced figs of *Ficus boliviana*[1] dominated their staple food source and therefore their overall nutritional intake. Our results suggest that spider monkeys consumed a diverse array of ripe fruits to overcome periods of fig scarcity.

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[1]. The taxonomy of this species is uncertain at the time of printing. This species may be *Ficus insipida* (synonym *F. glabrata*), but because the name *F. boliviana* is the accepted classification employed by Bolivian researchers I have chosen to use it throughout the thesis. Please contact the author for updated nomenclature.

4.2. Introduction

Primates must make choices regarding which foods to include in their daily diet, with these choices influencing their nutritional state and ultimately their health and fitness (Altmann 1998; Beehner et al. 2006). The food choices made will be determined primarily by the animal's regulatory phenotype, but constrained by the nutritional, chemical and structural composition of the foods in the environment (Milton 1993a; Lambert 2007). Quantifying the underpinnings of diet selection is challenging, especially in studies of wild animals, as it requires precise feeding observations of individuals over continuous periods, relevant analyses of all foods consumed, and a framework to analyse the complex, multivariate nature of the data.

The Geometric Framework for nutrition (GF) is an appropriate analytical technique (Raubenheimer & Simpson 2004), enabling an understanding of the nutritional strategies of animals (Simpson & Raubenheimer 1993), and the interpretation of food choices that are otherwise difficult to explain (Robbins et al. 2007). This framework has successfully been applied to a range of vertebrate and invertebrate taxa (Chambers, Simpson & Raubenheimer 1995; Simpson & Raubenheimer 2001;2005; Raubenheimer & Simpson 2006; Robbins *et al.* 2007; Ruohonen *et al.* 2007). The GF describes feeding behavior within an *n*-dimensional space delineated by axes representing nutrients of interest (Raubenheimer & Simpson 2004). It is possible to identify an animal's nutritional intake target within this nutrient space, and relate this target to the nutritional content of the foods available.

Ripe fruit is the main food of spider monkeys (genus *Ateles*, subfamily Atelinae). Spider monkeys are arboreal primates that inhabit the canopies of Neotropical forests (Kinzey 1997; Di Fiore et al. in press). Energy is often proposed to be the primary driver behind atelines' diet selection (Rosenberger & Strier 1989; Strier 1992; Di Fiore & Rodman 2001), because they frequently select and ingest large volumes of fruit that is rich in lipids and soluble carbohydrates (Castellanos 1995; Dew 2005; Di Fiore et al. in press). In contrast to this view and other major schools of thought in nutritional ecology (e.g. Schoener 1971; Freeland & Janzen 1974; Mattson 1980; White 1993; Dearing et al. 2005), Felton et al (Chapter 3) determined that spider monkeys (*Ateles chamek*) in La Chonta, Bolivia, selected diets that supply a set amount of protein, rather than attempting to maximize the ingestion of energy or protein, or to avoid plant secondary metabolites. Application of the GF revealed that daily protein intake was regulated more tightly than carbohydrates or fats, and thus disproportionately influenced total energy intake. Furthermore, protein intake did not vary across seasons despite dramatic fluctuations in food availability and the amount of leaves included in the diet (Chapter 3).

Research on this community of spider monkeys showed that although their diet contained as much fruit as other *Ateles* species, it differed in two respects (Chapter 2). First, figs (*Ficus*) were a staple food all through the year. There are no similar reports of a comparable reliance on *Ficus* by this primate genus even though all spider monkeys eat figs (Di Fiore et al. in press). Second, the spider monkeys in La Chonta spent much time consuming unripe figs, even when ripe figs and other ripe fruit were abundant.

In this paper, we build on the knowledge that diet selection of the La Chonta spider monkey community is governed by protein-dominated macro-nutrient balancing. We use the Geometric Framework to assess the influence of this nutritional strategy on daily and seasonal nutritional states of individuals by analyzing the intake trajectories of individuals and the macro-nutritional balance of foods consumed. We also estimate the nutritional value of different foods, and interpret in nutritional terms, the unusual food choices described above.

4.3. Methods

4.3.1. Study site and study design

We collected data in the lowland subtropical semi-humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia (Figure 2.1). The study area (S: 15° 36’ 26.3 to 15° 37’ 44.5 and W: 62° 46’ 58.9 to 62° 47’ 55.7) was located in the 100,000 hectare forestry concession “La Chonta”, owned by Agroindustría Forestal La Chonta Ltda. The average annual temperature and precipitation for La Chonta are 25°C and 1580 mm, with 4 dry months (<100 mm rain; May – September).

Tall forest dominates the study area, with small sections of low vine forest, chaparral and swamp (Chapter 2). There were three distinct phenological periods (“seasons”) during the study, including a period of high ripe fruit abundance (late wet season) followed by a ten-week period of fruit scarcity (early – mid dry season) before ripe fruit became more abundant again (late dry – early wet season; Chapter 2).

We established a network of trails in the study animals' 360-400 ha territory and used it for daily observations of focal animals, monthly phenological surveys and one vegetation survey. We collected basal area information from all trees over 10 cm diameter at breast height (dbh) within 71 0.1 ha plots distributed throughout the home range. A detailed description of the design and sampling of our phenology surveys appears in Chapter 2.

4.3.2. Feeding observations and food collection

We spent five months habituating the study community, and thereafter (from February 2004 to September 2004) systematically collected feeding data using continuous observations of a focal animal (FA) from dawn to dusk. We followed each of 18 FAs (8 males and 10 females) for at least one day each month, alternating daily between males and females. Females were either lactating or pregnant while caring for a juvenile. We recorded the time of the start and end of each feeding event, and the foods eaten from the categories of ripe fruit/ fig, unripe fruit/ fig, flower, young leaf, mature leaf, or other. We took detailed notes on which parts of the fruits were consumed. We used differences in fruit size, color and consistency to differentiate between immature and ripe fruits. We calculated feeding rates (number of items/ minute) for all food types. We identified and tagged all plants from which the monkeys ate. Within one or two days of feeding observations, we collected and dried (40-50°C) samples of the food items from these trees (see Chapter 3).

4.3.3. Analytical techniques

We used near infrared reflectance spectroscopy (NIRS) (Foley et al. 1998) to estimate the concentrations of total nitrogen, lipid, starch, neutral detergent fiber, ash, PEG binding capacity, and *in vitro* digestible nitrogen and dry matter (DM) in all food items. This was done using standard NIRS procedures (ANON 1995). Descriptions of chemical analyses of total nitrogen (total N), water-soluble carbohydrates, starch and neutral detergent fiber are provided in Chapter 3. Values for water-soluble carbohydrates and starch were combined and presented as total non-structural carbohydrates (TNC). Tannins were assayed as the amount of polyethylene glycol (PEG) bound per unit DM and we estimated the effect of tannins on nitrogen and DM availability using the *in vitro* digestion procedure described by De Gabriel and others (in press). We estimated "available protein" as (total N) x (*in vitro* N digestibility) x 6.25. We assumed that lipids were 100% available. Dry matter digestibility (DMD) is presented as DMD in the absence of PEG (DMD-PEG). We did not analyze termites but instead used the nutrient concentrations reported by Dufour (1987).

4.3.4. Use of the Geometric Framework

We applied the Geometric Framework (Simpson & Raubenheimer 1995; Raubenheimer & Simpson 1997) to our data. For the analysis of the macro-nutrient balance of food items and nutrient intake, we plotted available protein in energy units for the sake of uniformity. For this purpose, we calculated the energetic value of each food, using the following conversion factors: 0.0167 MJ /g TNC, 0.0377 MJ /g lipid, and 0.0167 MJ /g available protein. We acknowledge that the role of protein as an energy source to primates is minor but is predominantly used for growth and replacement of body tissue (Leonard 2000). Because TNC and lipids can be regarded as interchangeable energy sources for the purpose of this analysis (Ruohonen et al. 2007, and Chapter 3), we combined TNC and lipids into one axis (non-protein energy), with available protein energy on the other axis. We refer to this two-dimensional space as "the nutritional space". In this analysis we include only those focal days when *all* feeding events were documented in detail, and relevant analyses existed for every food consumed.

4.3.5. Data analysis

We estimated nutrient intake from each feeding event by multiplying the ingestion time with the corresponding feeding rate and the nutrient content of the item (for details see Chapter 3). We summed all daily events to obtain the daily nutrient intake. To compare differences in nutrient gain versus time spent feeding (nutrient intake efficiency, NIE) on ripe and unripe figs of *Ficus boliviana*, we divided the estimated total intake of nutrient *x* (g) from item *i* with the total time spent feeding (minutes) on item *i*.

We used linear regression to assess the relationship between feeding rates (population means of #items/min) and wet weight of immature and ripe figs belonging to the species *Ficus boliviana* and *F. trigona*. We used one way ANOVA to test differences in nutrient intake efficiency between unripe and ripe figs of *Ficus boliviana*. We assessed whether the mean observed intake ratio across all days ("OBS") was purely a product of the dominance of figs in their diet or whether the nutrient intake balance of individuals was the same regardless of the presence of figs. For this purpose, we used one-way ANOVA to test whether OBS (n = 38) was different from the observed daily intake ratio of days when figs were not consumed at all (n = 13). There was no significant difference between sexes or between individuals in daily nutritient intake (Chapter 3).

4.4. Results

Between February and September 2004, we followed focal animals for 51 full days (32 days of 8 females, 19 days of 8 males), and 19 partial follow days. There were no significant differences in macro-nutrient intake between sexes or individuals (Chapter 3). It is thus unlikely that the greater number of female follow days represented a bias in our analysis. We recorded 904 different feeding events, amounting to 175 hours of observation. During the 51 full day follows, we observed monkeys eating 84 different foods, 69 of which we collected and analyzed. Focal animals spent <1% of their total feeding time eating items we did not subject to chemical analysis.

4.4.1. Nutritional composition of food items

The *in vitro* measure of protein availability (and DM) may not accurately represent *in vivo* availability, but it at least allowed us to estimate the proportion of total nitrogen available to the consumer versus how much was bound up by dietary tannins. To highlight the disparity between concentrations and intakes of "available protein" (available N x 6.25) and "crude protein" (total N x 6.25), we include both measures in tables and appendices.

Ripe fruit usually contained almost 50% more TNC and lipids than did immature fruit, which instead contained more fiber and ash, had lower DMD, but similar concentrations of available protein (Figure 4.1). Young leaves contained more available protein and had higher DMD than did mature leaves (Figure 4.1). For figs, we refer to the emerging buds, immature figs and medium-ripe figs collectively as "unripe figs", because they had similar composition that was unlike that of ripe figs. Individuals consumed different combinations of wall/ pulp of ripe figs depending on the species of *Ficus*. The nutritional composition of the most commonly eaten combinations of figs and other items are presented in Appendix 2.

4.4.2. Feeding rates

We recorded 775 different feeding rates (including several replicates per feeding event), supplying information on the rate of ingestion of 76 different food items. This information was used in calculations of daily nutrient intake. Spider monkeys consumed small figs (i.e. less mature when comparing within species) faster than they did larger figs (data for *Ficus boliviana* and *F. trigona*, $R^2 = 0.70$, $n = 7$, $p = 0.011$).

4.4.3. Daily nutrient intake and major sources of nutrients

Spider monkeys ate 0.4 – 2.4 kg (mean 1.0 kg ; SE 0.07 kg) of fresh food per day, which corresponded to an average of 262 g (± 15 g SE) of DM (Table 4.1). Of the mean daily intake of DM, 34% was TNC, 4.4% available protein, 2.5% lipids, 6% inorganic material (ash) and 36% NDF (Table 4.1). The daily intake of available protein remained steady across all three phenological seasons (mean 11 g/day ± 0.76 g SE), while the intake of crude protein fluctuated with 75%.

On only 8 of the 51 full follow days did monkeys not eat *Ficus* fruits or leaves, with seven of these days occurring during the period of fruit scarcity. Spider monkeys predominantly used *Ficus boliviana* and *F. trigona*, but also ate figs from four less common *Ficus* species (Appendix 2). *Ficus* trees represented 23% of all food trees and focal animals spent 50% of their feeding time eating various items from *Ficus* (Table 4.1). This resulted in *Ficus* supplying the spider monkeys with the majority of their protein, lipids, fiber and water (Table 4.1). Other main sources of nutrients were *Pseudolmedia laevis* and *Myrciaria* sp. (locally called “sahuinto”; Table 4.1).

4.4.4. Seasonal differences in sources of nutrients

The relative contributions of different food categories to spider monkeys’ nutrient intake varied between the three phenological seasons (Figure 4.2), although ripe fruit was prominent in all seasons. During the period of relative ripe fruit scarcity, monkeys relied more on immature fruit and mature leaves than during the previous peak fruiting season (Figure 4.2b versus 4.2a). At the beginning of the next peak fruiting season, individuals changed from eating mature leaves to young leaves, but immature fruit (of which unripe figs constituted 84% of feeding time) still provided >20% of all nutrients except TNC (Figure 4.2c). The effect of these dietary differences is reflected in the average nutritional state of individuals during the study (Figure 4.3d). While protein intake remained stable across seasons, the abundance of TNC- and lipid-rich fruit in the habitat during the late peak fruiting season resulted in monkeys ingesting 52% more non-protein energy than they did in the period of fruit scarcity (their “fall-back diet”; Figure 4.2d).

4.4.5. Fig nutrition and macro-nutritional balance of food items

Figs were major sources of nutrients for focal animals during six of the eight sample months. Nutrient concentrations of figs varied greatly between species and stages of maturity (Appendix 2). Compared with other fruit, figs contained low to medium concentrations of lipids, available protein and TNC (Appendix 2). However, ripe figs of *Ficus boliviana* (one of the two most eaten fig species) have a macro-nutrient balance that resembles the intake trajectories of the spider monkeys (Figure 4.3). In contrast, most other ripe fruit had higher TNC and/or lipid content than these ripe figs (Figure 4.3). The mean observed ratio of the intake of protein energy to non-protein energy across all observation days did not differ significantly from the ratio on those days when monkeys did not eat figs ($n = 12$, $p = 0.155$). Besides the ripe figs of *Ficus boliviana*, two other types of figs and three kinds of non-fig fruit appeared to be nutritionally-balanced for the spider monkeys (Figure 4.3).

Most (88%) of the unripe figs that monkeys ate came from *Ficus boliviana*. These figs had high ratios of protein energy to non-protein energy (Figure 4.3), and had more available protein, lipid and ash than did the ripe figs of this species (Appendix 2). Although the ripe figs of *F. boliviana* contained higher concentrations of crude protein than did the immature figs, the reverse was true for available protein (Appendix 2). Also, spider monkeys ingested both available protein ($p < 0.001$) and lipids ($p = 0.039$) more efficiently (g nutrient ingested/minute feeding) when eating immature figs compared to ripe figs of *Ficus boliviana,* while there was no difference in the intake efficiency of TNC ($p = 0.11$). Spider monkeys always ate unripe figs in combination with other food types (mean 5.8 other food types ± 0.7 SE, range 1-10). Usually (79% of days), the “other food” was predominantly ripe fruit, rich in TNC and/or lipids (mean 55% of DM; SE = 7% SE). In the remaining cases, individuals supplemented their unripe fig consumption with nutritionally-balanced foods, such as ripe figs or palm fruit.

4.4.6. Daily tracking between feeding events

By assessing cumulative nutrient intake trajectories across consecutive feeding events, we found that individuals would attain an average balance between available protein and non-protein energy by: (*a*) staying on a straight intake trajectory by eating nutritionally-balanced foods (13% of days), or (*b*) mixing foods with high and low protein:non-protein ratios (83% of days). Alternatively, they would ingest more non-protein energy than average by: (*c*) staying on a straight intake trajectory while eating foods extremely rich in TNC and lipids (4%). Individuals were more likely to concentrate on nutritionally-balanced foods (option *a*) when ripe figs were abundant (Table 4.2). In contrast, individuals were more likely to mix complementary foods on a daily basis (option *b*) when both ripe figs and other ripe fruit were in moderate abundance. Finally, they were more likely to ingest extremely large amounts of non-protein energy (option *c*) when figs were scarce but other ripe fruits were abundant and therefore highly prominent in their diet (Table 4.2). We make the assumption that spider monkeys consumed “surplus” energy when using option *c*, i.e. more energy than needed to maintain body weight.

During the sampling periods when ripe fruit was abundant (late wet- and early wet seasons), there was a negative hyperbolic relationship between the availability of ripe figs and the mean number of different non-fig fruit types consumed per day (Figure 4.4). During these periods, individuals could choose whether to eat a multitude of ripe fruits, but they did so only when the availability of ripe figs was low (Figure 4.4).

Table 4.1. The relative contributions of ingested nutrients from the ten plant species most commonly consumed, and daily intakes of different nutrients. Data include 51 full day follows over the entire study with plant species sorted by the relative amount of dry matter ingested.

Species	Item	%DM	%water	%ash	%AP	%TNC	%lipids	%NDF	%time
TOP 10 SPECIES (of 47), representing 84% of all consumed dry weight.									
Ficus boliviana	EB,I,MR,R,LB,YL,L	22.8	15.6	34.2	23.2	10.1	25.6	31.6	28.0
Myrciaria sp.	MR,R	18.5	15.4	12.6	5.9	19.5	4.2	15.5	10.7
Pseudolmedia laevis	EB,I,MR,R,FB,YL	16.4	19.1	11.6	14.4	27.9	8.4	11.3	10.4
Ficus trigona	EB,I,MR,R,LB,YL	7.2	17.0	8.4	4.0	4.4	7.0	7.9	22.1
Spondias mombin	R	5.1	5.3	4.4	2.2	8.4	4.9	1.4	1.7
Guazuma ulmifolia	R	4.6	1.4	2.1	2.5	3.4	2.0	7.4	3.4
Jacaratia spinosa	R,F,L	4.1	5.3	3.4	8.6	6.4	3.5	3.0	1.4
Pouteria nemorosa	I,MR,R	3.6	6.1	2.8	2.2	6.2	5.2	0.6	3.1
Heliocarpus americanus	LB,YL,L	3.4	2.3	6.3	7.7	1.0	6.2	6.2	2.1
Batocarpus amazonicus	LB,YL	2.0	1.7	3.0	3.6	0.6	2.9	3.6	2.7
Genus *Ficus*	all items	31.3	33.2	43.6	27.7	15.4	33.3	40.2	50.8
		DM	**water**	**ash**	**AP (CP)***	**TNC**	**lipids**	**NDF**	
Mean daily intake		262g	1487g	15.7g	11.5g (17.2g)	88.4g	6.6g	94.5g	
SE of mean		15	103	0.9	0.8 (0.7)	10	0.5	6	
% of daily mean dwt intake				6.0%	4.4% (6.6%)	34%	2.5%	36%	

EB = emerging fruit bud; I = immature fruit; MR = medium ripe fruit; R = ripe fruit; F = flower; FB = flower bud; LB = leaf bud; YL = young leaf; L = mature leaf; %water = proportion of fresh weight; AP = available protein estimated from *in vitro* assay (available N x 6.25); TNC = total non-structural carbohydrates (water-soluble carbohydrates + starch); NDF = neutral detergent fiber; % time: percentage of total feeding time. *crude protein (CP = total N x 6.25) intake presented for comparative purposes.

Table 4.2. Ecological parameters that differed significantly between three different strategies which individuals used to reach their daily nutritional requirements.

	A: straight/ balanced	**B: switching/ balanced**	**C: straight/ surplus TNC+L**	**p-value****
Number of days*	4	32	2	
Diet composition				
mean % of diet consisting of non-fig fruit (±SE)	18 (±11)	45 (±5)	98 (±2)	0.007
mean % of diet consisting of figs (±SE)	80 (±13)	31 (±5)	0	0.005
Habitat-wide food availability				
Availability of ripe figs (score)	31	13	8	0.007
Availability of ripe non-fig fruit (score)	13	25	40	0.049

A: individuals followed a straight intake trajectory reaching a balanced end-point in nutritional space (see text for definition) by eating nutritionally-balanced foods. B: individuals reached a balanced end-point in nutritional space by alternating between complementary foods. C: individuals followed a straight intake trajectory but reached their daily end-point by ingesting a surplus of non-protein energy (TNC+L). * the analysis uses 38 of the 51 full day follows, i.e. those with detailed data from every feeding event. ** Results from one-way ANOVA.

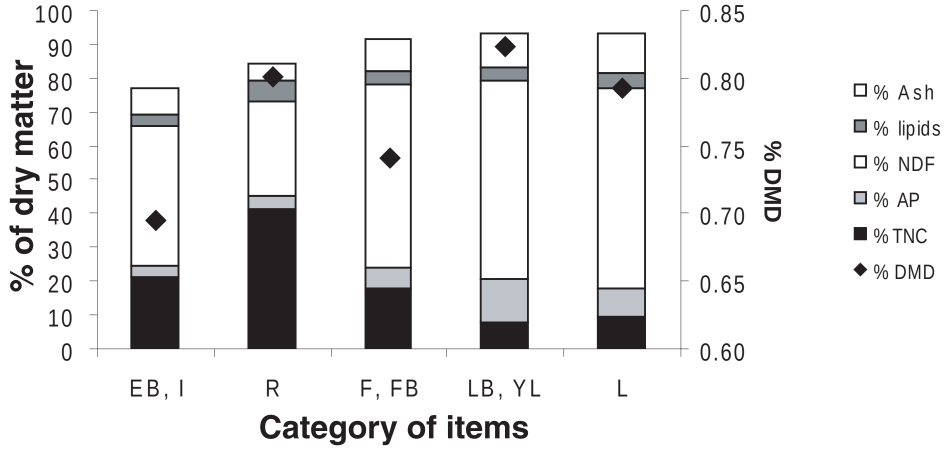

Figure 4.1. Average nutritional composition of food categories eaten by *Ateles chamek* in La Chonta. EB = emerging buds; I = immature fruit; R = ripe fruit; F = flowers; FB = flower buds; LB = leaf buds; YL = young leaves; L = mature leaves; NDF = neutral detergent fiber; AP = available protein; TNC = total non-structural carbohydrates; %DMD = in vitro DMD (see Methods).

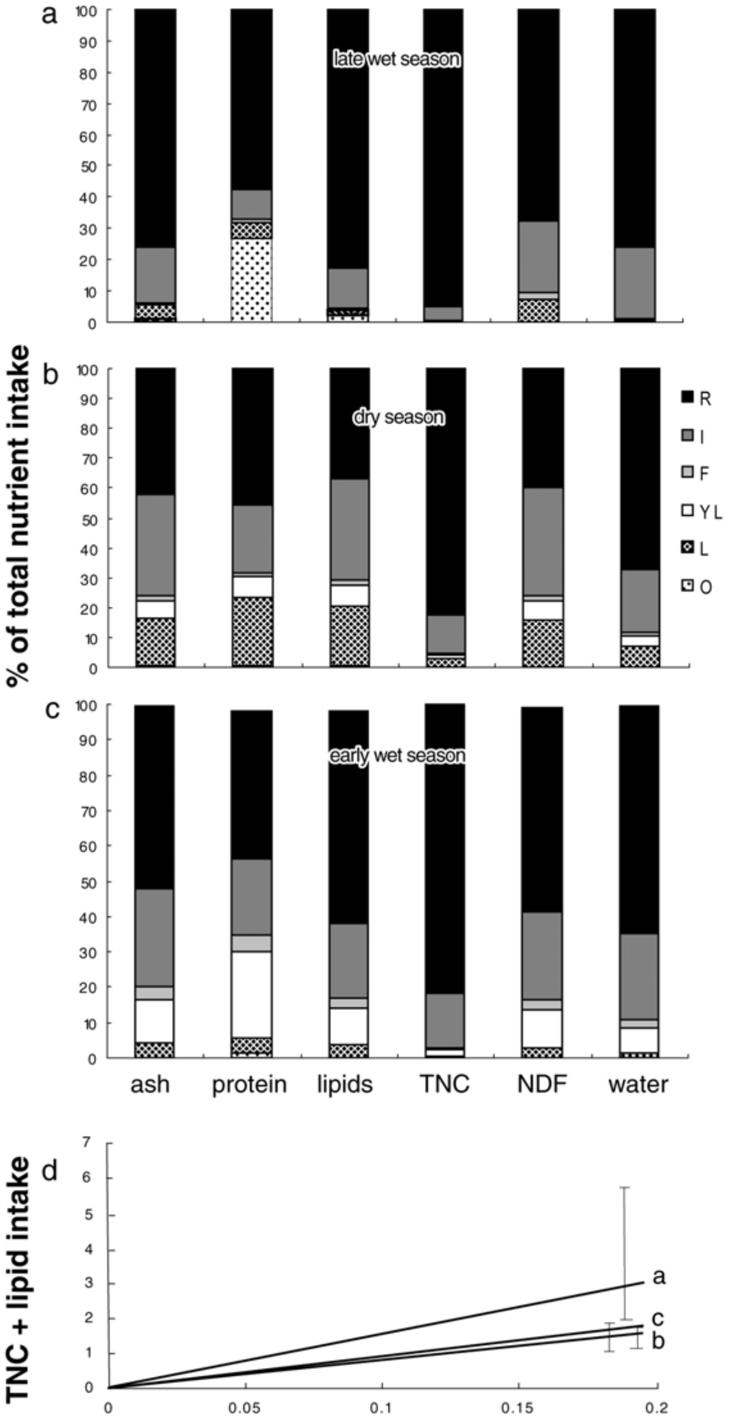

Figure 4.2. The contributions of different food categories to total nutrient intakes during three phenological periods (a-c), and the associated mean macro-nutrient intake balance (d). a) Late wet season; b) Early-mid dry season; c) Late dry-early wet season. For explanations of abbreviations of food categories see Figure 4.1 (O = other); d) Mean seasonal intake ratios of available protein

versus non-protein energy that result from changing dietary composition in seasons a-c. Vertical bars indicate 95% confidence limits.

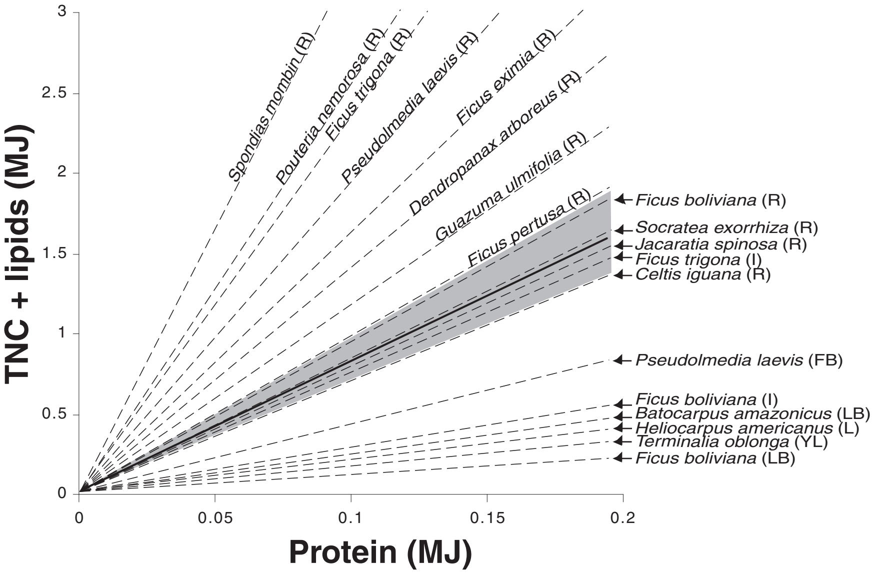

Figure 4.3. The ratios of the available protein energy versus non-protein energy of the 17 most commonly eaten foods (food rails: dashed lines), in relation to the mean observed intake ratio across all observation days (solid line, 95% confidence intervals depicted with a shaded area). Food rails represent the macro-nutritional balance of a food and show the intake trajectory of an animal that is restricted to this food item. Two additional species of *Ficus* have also been included for comparison. The mean observed intake ratio did not differ significantly from the intake trajectory of those days when monkeys did not eat figs (n = 12, p = 0.155). R = ripe fruit; I = immature fruit; L = leaves; YL = young leaves; LB = leaf buds; FB = flower buds.

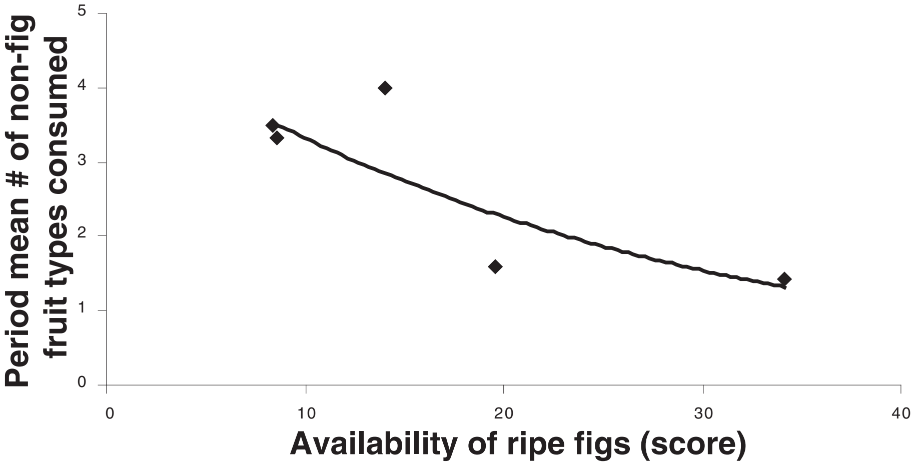

Figure 4.4. The hyperbolic relationship between habitat-wide availability of ripe figs and the mean number of non-fig fruit types consumed ($R^2 = 0.72$). During the periods when individuals could choose to include a multitude of ripe fruits in their diet (late wet season (n = 3 phenological surveys), and early wet season (n = 2)) they did so only when ripe figs were rare.

4.5. Discussion

Spider monkeys ate food items of widely varying macro-nutrient composition (Appendix 2, Figure 4.3). Despite this variation, individuals often managed to ingest a similar daily balance of available protein and non-nitrogenous energy sources. We consider this mean ratio to be their “preferred region of nutritional space”, as it appears to be defended by individuals in the face of large variation in diet composition (Simpson & Raubenheimer 1993;1995). They reached this point in nutritional space either by consuming a small number of “nutritionally-balanced” foods over the course of a day (here: foods that have a ratio of available protein:(TNC+lipids) similar to their observed mean intake), or by alternating between nutritionally complementary foods that contained either high or low ratios. We discuss each of these alternatives in turn.

Consuming nutritionally-balanced foods represents the most direct route to a preferred region of nutritional space. Three types of figs were nutritionally-balanced, as were food items from three other plant species: ripe fruit of the tree *Jacaratia spinosa*, the liana *Celtis iguanea* and the palm *Socratea exorrhiza* (Figure 4.3). Of these plant species, figs played a disproportionately large role in the spider monkey’s diet. Spider monkeys spent 45% of their feeding time eating figs that provided them with approximately a third of their total intake of lipids and available protein (Table 4.1). Individuals were more likely to follow a straight intake trajectory towards a balanced macro-nutritional end point when ripe figs were highly abundant and made up a large proportion of their diet (Table 4.2).

We suggest that there are several reasons why figs played a pivotal role in the diet of these spider monkeys. First, *Ficus boliviana* and *F. trigona* were relatively common in their territory (Appendix 2) and produced large fruit crops for eight to nine months of the year (Chapter 2). Second, our findings suggest that these figs are balanced nutritionally in relation to the spider monkeys’ nutritional target. As such, the nutrient balance of figs may be more indicative of their value than are the concentrations of individual macro-nutrients *per se*, which are generally moderate to low (Appendix 2, Jordano 1983; Herbst 1986; Conklin & Wrangham 1994). Third, figs contained high concentrations of inorganic material, presumably minerals (“ash”; Appendix 2) and contributed 44% of their total intake of inorganic material (Table 4.1). Figs are known to be extremely rich sources of available calcium (Duhan, Chauhan & Punia 1992; O'Brien *et al.* 1998; Ruby *et al.* 2000; Wendeln, Runkle & Kalko 2000), which is critical for maintenance and reproduction (Robbins 1993). We suggest that all of these factors contributed to figs being the staple food of spider monkeys in La Chonta. Interestingly, the spider monkeys included a large number of other ripe fruit types in their diet only when ripe figs were scarce, despite the opportunity to do otherwise (Figure 4.4). There is a common perception that tropical frugivores regard figs as critical fall-back foods, rather than as preferred foods when other options are available (Milton et al. 1982; Shanahan et al. 2001). Our results are not congruent with this opinion and indicate that these spider monkeys eat a diverse array of different fruit to endure periods of fig scarcity (see also Kinnaird & O'Brien 2005). We tentatively suggest that the unusually large size of this spider monkey community (55 individuals, mean for *Ateles* communities is 31, see Campbell in press for comparisons with other spider monkey study communities) is partly attributable to the preponderance of this nutritionally-balanced and mineral-rich staple food.

If nutritionally-balanced foods were not sufficiently available for monkeys to meet their daily requirements, individuals could reach their preferred region in nutritional space by eating nutritionally imbalanced complementary foods. Although this feeding strategy was by far the most commonly used (84% of cases), it may have associated costs. Repeated alternation between foods involves lost feeding time, increased risk of predation, and presumably higher energetic costs of locomotion (Dunbar 1988; Chambers et al. 1995). Individuals were more likely to employ this switching strategy when ripe figs and other ripe fruit were of low to moderate availability (Table 4.2). For example, monkeys always used the switching strategy during the early-mid dry season when ripe fruit was scarce. Leaves were frequently part of this fall-back diet and individuals would systematically alternate between leaves and the few ripe fruits available. Notably, the presence or absence of leaves and flowers in the diet did not influence the daily protein intake of these monkeys (Chapter 3). It is often stated that frugivorous primates must eat some leaves to obtain sufficient protein (Milton 1981; Oftedal 1991; Milton 1993a; Chapman & Russo 2007; Lambert 2007; Strier 2007). Our results show that this is not the case for spider monkeys, at least on a daily basis, because they consistently reached the protein intake target even when eating only ripe fruit.

During the late wet season when ripe fruits were highly abundant, individuals consumed large amounts of fruit rich in TNC and/or lipids ("energy-dense" fruit, e.g. *Spondias mombin* and *Pouteria nemorosa*) resulting in a dramatically higher total energy intake than average (Figure 4.2d). We hypothesize that the spider monkeys took advantage of these peak season foods by ingesting surplus energy and storing it as fat in preparation for the impending period of food scarcity when total energy intake halved. Other ateline species (*Lagothrix lagotricha cana*: Peres 1994a; *Ateles chamek*: Wallace 2005) are known to accumulate fat during periods of peak fruit abundance and it is a logical strategy for animals experiencing fluctuating food supply. Seasonal accumulation of fat reserves may be crucial for survival and reproduction in spider monkeys and we therefore suggest that bulk-up foods should be given appropriate attention in conservation planning (see also Knott 1998; Stevenson 2005).

The framework of protein-dominated nutrient balancing can be used to unravel food choices that are difficult to explain using traditional schools of thought in nutritional ecology. For example, in contrast to other spider monkey communities studied, the spider monkeys at La Chonta spent much time consuming unripe figs (18% of feeding time, primarily from *Ficus boliviana*) both during periods of abundance and scarcity of ripe figs and other fruit (Chapter 2). When ripe figs and other fruits were scarce the consumption of unripe figs was likely a matter of availability (Norconk et al. 1998; Schaefer & Schaefer 2006). During this study, unripe figs were always available in the home range making them a more reliable food source than ripe figs (Chapter 2). The more intriguing issue is why spider monkeys ate figs when ripe figs and other fruits were available.

Ripe-fruit specialists often avoid unripe fruits because they are usually less palatable than ripe fruit (Venu et al. 2005), contain less gross energy (Schaefer, Schmidt & Winkler 2003), and often contain toxins or anti-feedants (Cipollini & Levey 1997a;b). Some of this may be true for the unripe figs in this study but, importantly, the unripe figs of *Ficus boliviana* provided spider monkeys with more lipids and available protein per minute feeding than did their ripe counterparts. This greater efficiency was due to the high concentrations of lipids and available protein (the latter likely enhanced by the inclusion of protein-rich wasp bodies (Herbst

1986)), and the speed at which monkeys could consume unripe figs. Furthermore, our data show that the consumption of unripe figs always occurred in combination with other food types, and usually the alternative foods contained relatively high concentrations of non-protein energy. Unripe figs thus constituted an easily harvestable, nutritionally rewarding, and continuously available complementary food.

Implications of our findings to primate nutritional ecology

Understanding diet selection is a subject that has intrigued nutritional ecologists for a long time. The geometric framework is a novel approach to this issue as it facilitates an increased understanding of the nutritional underpinnings of diet selection. Its application also provides a lens through which to determine the relative value of different foods, and how this value might relate to phenological patterns. We therefore encourage other primate ecologists to adopt the geometric framework in their studies of the diets of wild primates.

Our results provided further insight into why figs often play a pivotal role in the diets of tropical frugivores. Moreover, our study provided an exception to the general rule that figs are a less-preferred food that assists animals in overcoming lean periods. Instead, for our study animals, figs were a readily available, nutritionally-balanced and mineral-rich staple food resource. Access to this food resource allowed individuals to sometimes concentrate their feeding in a few trees and thus most likely reduce energetic costs and predation risk. In contrast to prevailing theory, the spider monkeys at La Chonta consumed a diverse array of different fruits to endure periods of fig scarcity.

4.6. Acknowledgements

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Photo by Kristen Evans

This forest giant, *Ficus boliviana*, served as a regular feeding and resting tree for the spider monkeys

Chapter 5 – Timber tree species play a critical role in the nutritional ecology of spider monkeys (*Ateles chamek*) in a certified logging concession, Bolivia

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5.1. Abstract

Selective harvesting of timber is applied over large areas of tropical forest every year. The resultant changes to these forests can have negative repercussions for forest dependent biota. For example, selective logging can remove significant amounts of food resources for primates, leading to declines in primate population densities. As frugivorous primates are important seed dispersers in tropical forests, it is critical for the long-term ecological sustainability of forestry concessions to maintain primate populations. In this paper, we quantify the importance of timber tree species (TTS) in the diet and nutritional ecology of spider monkeys (*Ateles chamek*) inhabiting the certified forestry concession La Chonta in Bolivia. This concession applies reduced-impact logging procedures. Other researchers in this forest have found recently logged areas to sustain 25% of the spider monkey population densities found in unlogged areas. We show that spider monkeys occupying unlogged areas obtained approximately 50% of their total intake of macro-nutrients from TTS. Timber tree species comprised the staple food of spider monkeys, and dominated their diet both during peak fruiting periods and during periods of fruit scarcity. Spider monkeys exhibited a distinct preference for foraging within individuals of TTS that were of harvestable size. We estimated that under current timber extraction intensities, spider monkeys lose significant proportions of their food sources. Our results indicate that extraction limits should be considered for the timber tree species *Ficus boliviana*[1], *Spondias mombin* and *Pouteria nemorosa*. Our findings suggest that to ensure long-term ecological sustainability of certified forestry concessions, the importance of timber tree species in the ecology of seed dispersers needs to be taken into account.

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[1]. The taxonomy of this species is uncertain at the time of printing. This species may be *Ficus insipida* (synonym *F. glabrata*), but because the name *F. boliviana* is the accepted classification employed by Bolivian researchers I have chosen to use it throughout the thesis. Please contact the author for updated nomenclature.

5.2. Introduction

Approximately six million hectares of tropical forests are opened up annually for the first time to selective logging (Bennett 2000; Chapman & Peres 2001), although this estimate is highly conservative (Asner et al. 2005; Foley et al. 2007). While selectively logged forests maintain some forest cover, biota can be directly impacted by structural changes to their habitat, changes to microclimatic conditions, altered or reduced food resources, and interrupted ecological processes (Fimbel, Grajal & Robinson 2001). These changes can lead to significant population declines of some forest-dependent animal species (see reviews in Grieser Johns 1997; Bawa & Seidler 1998).

Empirical studies focussing on non-human primates have shown that selective logging can remove significant amounts of food resources for primates (Johns 1986; Marsh, Johns & Ayres 1987; Oates 1996; Felton *et al.* 2003), alter the nutritional quality of their food (Rode et al. 2006), and disrupt their canopy pathways (Marsh et al. 1987; Gebo & Chapman 1995; Felton et al. 2003). These modifications have been proposed as explanatory factors contributing to observed primate population declines in selectively logged forests (Cowlishaw & Dunbar 2000). The primates that appear to be most sensitive to habitat disturbance such as logging are arboreal, large-bodied and wide-ranging species with slow reproductive rates that are highly dependent on ripe fruit (e.g. spider monkeys, genus *Ateles*) (Skorupa 1986; Johns & Skorupa 1987; Symington 1988b; Peres 1994b; Sorensen & Fedigan 2000).

There have been no detailed studies of the effects of logging on primates in the Neotropics (Plumptre & Grieser Johns 2001). However, surveys conducted in the certified forestry concession La Chonta, Bolivia, showed that forest that had been logged one and two years previously sustained only 25% of spider monkey (*Ateles chamek*) population densities found in comparable unlogged sections of the forest (Fredericksen et al. 2007). Although long-term data are lacking, the territoriality and slow reproductive rate of this species suggest that such dramatic changes in population densities are of serious concern. This significant difference in spider monkey density occurred despite the fact that reduced-impact logging (RIL) techniques were employed. Reduced-impact logging is a modified form of selective logging that incorporates a variety of techniques aimed at lowering levels of damage to the residual stand with the implicit assumption that these actions, in combination with strict hunting bans, will reduce logging-related impacts on biodiversity (Heinrich 1995; Uhl et al. 1997; Putz et al. 2001).

It is important that appropriate adjustments are made to minimize RIL-associated impacts on spider monkeys. There is evidence that declines in frugivorous primate populations can have deleterious effects on forest recovery and regeneration (Chapman & Chapman 1996; Chapman & Onderdonk 1998). This may, in turn, affect the long-term sustainability of forestry concessions. Spider monkeys are efficient seed dispersers (Dew 2001) that are known to ingest seeds of several timber species (Wallace 1998, Chapter 2). Spider monkeys often deposit seeds far away from the parent plant with a widely scattered spread on the ground, and thereby contribute to a relatively high survivorship of the seeds (van Roosmalen 1985; Zhang & Wang 1995; Forget & Sabatier 1997; Andresen 1999; Dew 2001; Stevenson et al. 2002; Russo et al. 2005).

In this paper, we document the role of timber tree species in the diet and nutritional ecology of *Ateles chamek* in the La Chonta forestry concession. We acknowledge that primates also may be affected by changes to vegetation structure caused by selective logging. However, we focus on food resources, as evidence suggests that structural changes play a minor role in explaining logging-related impacts on spider monkeys (Green 1978; Chapman et al. 1989). We quantify the contributions of timber tree species to three food/ diet categories:

(i) *staple foods*: foods which are fed upon all year-round independently of the availability of preferred foods (Knott 2005; Marshall & Wrangham 2007).

(ii) *peak season diet*: foods consumed during the period of peak fruit abundance

(iii) *fall-back diet*: foods of high abundance consumed when preferred foods are scarce (Marshall & Wrangham 2007).

We also assess the proportion of trees used by spider monkeys that were large enough to legally be harvested under RIL prescriptions. We set our findings in the context of actual timber extraction rates from this forest and speculate what the impact of RIL may be on food resources for this species.

5.3. Methods

5.3.1. Description of study area and subjects

5.3.1.1. Study area

The study area (S: 15° 36’ 26.3 to 15 37 44.5 and W: 62° 46’ 58.9 to 62 47 55.7) was located in the 100,000 hectare forestry concession La Chonta, part of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia (Figure 2.1). This concession is owned and managed by Agroindustría Forestal La Chonta Ltda, and certified by Smartwood©. This forest is transitional between dry forest and Amazonian wet forest and is described as a lowland semi-deciduous tropical moist forest (Peña-Claros et al. 2007). The dominant vegetation type in the study area was tall forest, but small sections of low vine forest, chaparral and swamp also occurred (Chapter 2). The average annual temperature for La Chonta is 25°C and average annual precipitation is 1580 mm, with 4 months receiving <100 mm (May – September). The seasonal distribution of rainfall during this study was representative of the average monthly rainfall for the forest (Chapter 2).

Three distinct phenological periods (“seasons”) were detectable in this forest during the course of this field study. These included an initial period of high ripe fruit abundance (late wet season) followed by a ten week long period of fruit scarcity (early – mid dry season) before ripe fruit became more abundant again (late dry – early wet season; Chapter 2).

The entire concession was subjected to legal and illegal selective logging of mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela odorata*) 10 – 25 years prior to this study (Fredericksen 2000; Quevedo 2006). Our particular study area had not yet been affected by more recent logging, and was situated at least 2 km from logged areas. The closest active timber harvesting was more than 8 km to the west of the study area and noise associated with felling operations was not audible to the researchers. Hunting is strictly prohibited and enforced within the concession.

5.3.1.2. Study subjects

Spider monkeys (genus *Ateles*, subfamily Atelinae) are found in varying forest types from Amazonian ever-green rainforest to deciduous forests throughout Central and South America (Kinzey 1997). They are diurnal, arboreal, frugivorous, and large-bodied primates (7.5-9kg) (Kinzey 1997; Smith & Jungers 1997). The largest social unit of the spider monkey society is called *community*, normally including 15 – 40 individuals (Campbell in press). All members of the community are rarely observed together as they split into subgroups according to a fission-fusion pattern of social structure (van Roosmalen 1985; Symington 1988c; Chapman 1990). We studied one community of spider monkeys consisting of 48-55 individuals, using a territory of 360-400 ha. Spider monkeys contribute with the largest proportion of primate biomass in this forest which is also inhabited by four other primate species (Wallace et al. 2000).

5.3.1.3. Harvesting procedure

Every year, approximately 2500 ha is harvested in La Chonta over three contiguous 850 ha blocks (~4km x 2km), yielding 50,000 m^3 of timber products (Jackson et al. 2002). Average harvest intensity in this forest is approximately 4 trees/ha, estimated average harvest volumes are 6 m^3/ ha, and the intended rotation time is 25 to 30 years (Jackson et al. 2002; Peña-Claros et al. 2007). About 160 tree species >10 cm diameter at breast height (dbh) have been identified at La Chonta, 23 of which are commercially valuable (Peña-Claros et al. 2007).

One year prior to logging, the forestry company conducts an inventory of harvestable trees. Trees that are selected for felling are cleared of all vines and climbers on or near the bole during the inventory. The minimum size for harvest (MCD = minimum cut diameter) is 50 cm dbh for all species except *Ficus boliviana* and *Hura crepitans*, which are harvested only when above 70 cm dbh. Approximately 20% of target species above minimum size for cutting are left as seed trees and future crop trees (Jackson et al. 2002).

The territory of our study community was part of a block that was inventoried for harvestable trees during 2005 and subsequently logged in 2006, i.e. two years after the completion of our data collection. In this paper, we include information given to us by the logging company (Agroindustría Forestal La Chonta Ltda) regarding the inventory of this block and the consequent extraction of timber from all three blocks logged during 2006.

5.3.2. Study design

We established a trail network in the study community's territory, which covered an area of approximately 360 – 400 ha. We used these trails for daily follows of focal animals, monthly phenology surveys and a detailed vegetation survey. Within 71 0.1 ha plots distributed throughout the home range, we collected basal area information from all trees over 10 cm dbh. Tree density and basal area information derived from this vegetation survey indicate the relative availability of certain food and timber species within the territory. For a detailed description of the design and sampling effort of our phenology surveys see Chapter 2.

5.3.3. Feeding observations

We spent five months habituating the study community. Following habituation, we systematically collected feeding data, between February 2004 and September 2004. We conducted continuous observations of the same focal animal (FA) from dawn to dusk. We followed each FA (8 males and 10 females) for at least one whole day each month. All females were either lactating or pregnant while caring for a dependent juvenile. In the nutritional analysis, we only included days where (i) the FA was successfully followed all day ("full follow days"); (ii) all feeding events were documented in detail, and (iii) where relevant analyses existed for every food item consumed. We collected data continuously on the FA's activities and noted the exact start and end time of each feeding event. Feeding rates (number of items/ min) were documented for all food types. We identified and tagged all plants that the monkeys ate.

5.3.4. Food collection and laboratory analysis

We collected food items from trees marked as feed trees and dried samples in a drying oven (40-50°C). We transported samples to The Australian National University where they were ground and analyzed. A sub-sample of food items were chemically analyzed for concentrations of total nitrogen, lipid, water-soluble carbohydrates, starch, neutral detergent fiber, ash, PEG-binding (polyethylene glycol) capacity, and *in vitro* digestible nitrogen and dry matter (DM). We estimated "available protein" as (total N) x (*in vitro* N digestibility) x 6.25. We assumed that lipids were 100% available. Values for water-soluble carbohydrates and starch are combined and presented as total non-structural carbohydrates (TNC). For a detailed description of sample preparation and laboratory analyses, see Chapter 3.

5.3.5. Data analysis

Nutrient intake from each feeding event was estimated by multiplying the ingestion time with the corresponding feeding rate and the amount of nutrient present per item (for details, see Chapter 3). We summed all daily feeding events to obtain the daily nutrient intake and calculated the nutritional contributions of each plant species per season. We calculated the percentage of the population of each timber tree species that were observed to be used during the study period. We estimated the loss of such "used trees" from the spider monkey territory under three different harvesting rate scenarios: (A) mean rates from the entire 2006 logging area; (B) mean rates from 1998 logging blocks (data reported in Pariona, Fredericksen & Licona 2003), and (C) the maximum legal harvesting limit which is 80% of existing harvestable trees equal or above minimum cut diameter (M. Peña-Claros, pers. comm).

5.4. Results

5.4.1. Annual contributions of timber tree species to diet

Spider monkeys were observed to consume fruit, leaves and flowers from 63 species of plants. Ten of these species (16%) were commercial timber tree species (TTS) that are logged in the concession (Table 5.1). Spider monkeys spent 47% of their feeding time in TTS, predominantly in *Ficus boliviana* (Moraceae) and *Pseudolmedia laevis* (Moraceae; Table 5.1). TTS provided individuals with approximately 50% of their total intake of non-structural carbohydrates (TNC), lipids and available protein (Table 5.1). Daily intake of food items from TTS ranged between 0 - 100% of total dry mass.

Spider monkeys ingested whole seeds of TTS and defecated them intact. In no instance did we observe mastication of seeds. In some cases, spider monkeys ingested small emerging fruits of *Ficus boliviana* and *Pseudolmedia laevis* (3.8% and <0.1% of fruit eating time respectively), whose seeds may have been vulnerable to digestion due to their immaturity.

5.4.2. Contributions of timber tree species in seasonal diets

Ficus boliviana played a major role in the diet during 6 of the 8 sample months (Table 5.1), making it a staple food source. This species provided spider monkeys with more available protein, lipids, fiber, inorganic material and water than any other plant species in this study (Table 5.1). Spider monkeys obtained almost 90% of their non-protein energy (TNC + lipids) from fruits of TTS, primarily sourced from *Spondias mombin* (Anacardiaceae) and *Pouteria nemorosa* (Sapotaceae), during the late wet season when the general availability of ripe fruit was high in the territory (their late peak season diet, Table 5.2). During the 10-week long period of relative fruit scarcity (the early-mid dry season), TTS were part of the fall-back diet and provided spider monkeys with a third (31%) of their available protein, and almost half of their lipids, primarily sourced from *Ficus boliviana* (Table 5.2). We refer to the diet eaten during the late dry – early wet season, when ripe fruit became more abundant again, as their early peak season diet. Timber tree species contributed with 60% of available protein and 67% of TNC to the early peak season diet.

5.4.3. Sizes of food trees/ timber tree species

Of the 544 tagged food plants used by the spider monkeys (excluding lianas and palm trees), 58% were TTS. Seventy-five percent of the tagged *Ficus boliviana* individuals were equal or larger than MCD (Figure 5.1). Spider monkeys used *Ficus boliviana* trees that were as large as 300 cm dbh and as small as 22 cm dbh (mean = 131 cm, stdev = 69cm, *n* = 56, Figure 5.1). The majority of tagged individuals of *Pouteria nemorosa* (91%) and *Spondias mombin* (77%) were equal or larger than MCD, whereas only 13% of *Pseudolmedia laevis* individuals were equal or larger than MCD (Figure 5.1).

5.4.4. Harvesting information from La Chonta

5.4.4.1.Inventory

At least four of the spider monkeys' major food species (contributed with >2% of total dry matter intake) were included in the logging company's inventory conducted one year before harvesting and therefore judged to be in demand as timber sources: *Ficus boliviana*, *Pseudolmedia laevis*, *Spondias mombin*, and *Pouteria nemorosa*. Five minor food species (contributed with ≤2% of total dry matter intake) also were among the tree species inventoried prior to logging (Table 5.1).

5.4.4.2.Timber extraction

During the 2006 harvesting season, 2136 trees were extracted from 2445 ha in total, partly overlapping with our study area. Average harvesting intensity was 0.87 trees/ ha and 3.2 m^3 wood/ha. Of the harvested trees, 20% of stems belonged to species used as food sources by the spider monkeys during the study period (Table 5.3). Averaged across the whole logging area of 2006, *Ficus boliviana* was harvested at a rate of 5.6 trees/ 100 ha and was the 5th most commonly extracted tree species (Table 5.3).

5.4.5. Estimations of harvesting rates from spider monkey territory

Based on measurements of tree density, we estimated the number of individual trees that existed within the spider monkey territory that belonged to the four TTS/ major food species and that were larger than MCD. During the study period, we observed the spider monkeys to use between 4% and 8% of these trees (Table 5.4). The estimated loss of such "potentially used trees" from the spider monkey territory varied greatly between the three different harvesting rate scenarios (Table 5.4). For example, under scenarios A (based on extraction data from 2006) and B (data from 1998) the spider monkey territory was estimated to lose between 4%- 32% of "potentially used trees" of *Ficus boliviana*, 0%-20% of *Spondias mombin* and 2% - 43% of *Pseudolmedia laevis* (Table 5.4).

Table 5.1. The contributions by ten commercial timber tree species to the total nutritional intake by spider monkeys. Full follow days were used in this summary (*n* = 51).

Species	Family	Items consumed[a]	% time	% DM	% water	% ash	% AP	% TNC	% lipids	% NDF	BA/ha	# trees/ha	# m
Ficus boliviana C.C. Berg	Moraceae	EB,I,MR,R, LB,YL,L	28.59	22.78	15.6	34.2	23.2	10.1	25.6	31.6	1.6	1.9	6
Pseudolmedia laevis J. F. Macbride	Moraceae	EB,I,MR,R, FB,YL	9.36	16.41	19.1	11.6	14.4	27.9	8.4	11.3	4.4	109.3	3
Pouteria nemorosa[b] Baehni	Sapotaceae	R	4.08	3.58	6.1	2.8	2.2	6.2	5.2	0.6	0.6	6.1	2
Batocarpus amazonicus (Ducke) Fosb.	Moraceae	R,YL,L	2.28	2.04	1.7	3.0	3.6	0.6	2.9	3.6	0.1	0.9	1
Spondias mombin L.	Anacardiaceae	R	1.94	5.08	5.3	4.4	2.2	8.4	4.9	1.4	0.3	1.5	2
Ampelocera ruizii[b] Klotzsch	Ulmaceae	R,YL,L,F	0.3	0.28	0.08	0.18	0.72	0.02	0.12	0.14	1.6	19.0	4
Terminalia oblonga (Ruiz & Pavón) St.	Combretaceae	YL,L	0.09	1.17	1.0	2.2	2.8	0.3	2.1	2.1	1.7	17.0	2
Caesalpinia pluviosa DC.	Caesalpiniaceae	YL	0.01	0.03	**	**	**	**	**	**	0.3	4.3	1
Pouteria macrophylla[b] (Lam.) Eyma	Sapotaceae	R	*	*	*	*	*	*	*	*	0.9	13.6	*
Cordia alliodora[b] (Ruiz & Pavón) Oken	Boraginaceae	R	*	*	*	*	*	*	*	*	0.3	3.6	*
Timber Tree Species Total			47	51	49	58	49	54	49	51			

Column headings: Items consumed: EB = emerging fruit bud; I = immature fruit; MR = medium ripe fruit; R = ripe fruit; F = flower; FB = flower bud; LB = leaf bud; YL = young leaf; L = mature leaf; %time = percentage of total feeding time incl. partial follow days; %DM = percentage of total dry matter intake, incl. partial follow days; water = proportion of fresh weight; AP = available protein estimated from in vitro assay (available N x 6.25); TNC=total non-structural carbohydrates (water-soluble carbohydrates + starch); NDF = neutral detergent fiber; #trees/ha = density of species as an average across the entire territory of the study community; BA/ha = basal area (m^2) per ha; m = number of months the species occurred in the diet of spider monkeys (total = eight months of detailed data collection); Notes: a = observations from the entire study period including habituation; b = the relative importance of species to spider monkey diet may have been underestimated as their fruiting period overlapped only partially or not at all with behavioral data collection, or their crop was damaged during 2004 (*Pouteria nemorosa*); * Feeding observations were made during habituation, therefore no detailed information available; ** no observations during full follow days.

Table 5.2. Seasonal use of timber tree species (TTS) by spider monkeys in La Chonta. Data from full day follows were used for this summary (*n* = 51).

Seasonal diet	**Items consumed**	**%time**	**%DM**	**%water**	**%ash**	**%AP**	**%TNC**	**%lipids**	**%NDF**
LATE PEAK SEASON DIET (Late Wet Season; 5 FAD; 24/2-6/4)									
Spondias mombin	R	22.6	45.8	36.8	44.1	20.8	47.5	38.3	36.6
Pouteria nemorosa[a]	R (MR+R)	45.1	35.0	46.0	31.0	23.0	37.5	44.0	18.2
Ficus boliviana	I,R	5.2	5.5	3.3	10.4	7.3	1.2	5.8	21.7
% TTS of season total		73	86	86	85	51	86	88	77
FALL-BACK DIET (Early-mid Dry Season; 19 FAD; 10/4-28/6)									
Ficus boliviana	EB,I,R,YL	28.8	25.5	18.6	35.1	24.1	10.3	37.5	36.5
Batocarpus amazonicus	LB+YL	4.0	3.2	2.8	4.2	5.5	1.1	5.4	5.2
Pseudolmedia laevis	FB	7.8	1.1	0.9	1.8	1.3	0.5	1.6	1.5
Spondias mombin	R	0.5	1.1	1.2	0.9	0.5	2.1	1.3	0.3
% TTS of season total		41	31	23	42	31	14	46	44
EARLY PEAK SEASON DIET (Late Dry - Early Wet Season; 27 FAD; 12/7-15/9)									
Pseudolmedia laevis	R,FB,MR,EB,I,YL	13.5	30.2	35.8	21.8	26.3	54.3	14.6	18.9
Ficus boliviana	LB,EB,R,MR,I	30.1	22.7	15.7	35.3	24.4	11.3	23.7	27.6
Terminalia oblonga	YL,L	0.2	2.2	1.9	4.3	5.5	0.5	3.9	3.6
Batocarpus amazonicus[a]	LB+YL	2.2	1.7	1.5	2.7	3.1	0.6	2.5	2.9
Ampelocera ruizii[a]	YL	0.3	0.2	0.1	0.3	1.2	0.0	0.2	0.2
% TTS of season total		46	57	55	65	60	67	45	53

Column headings: see explanations in Table 5.1. Notes: a = the relative importance of species to spider monkey diet may have been underestimated as their fruiting period overlapped only partially or not at all with behavioral data collection (*Ampelocera ruizii*, *Batocarpus amazonicus*), or their crop was damaged during 2004 (*Pouteria nemorosa*).

Table 5.3. Timber species inventoried and/ or extracted from La Chonta during 2006. Species are sorted by harvesting intensity. Also indicated is whether these timber species provided food for spider monkeys during the study period.

Tree species	Family	# trees / 100 ha[a]	% of total[b]	Food source
Cariniana ianeirensis Knuth	Lecythidaceae	28.1	32.2	no
Hura crepitans L.	Euphorbiaceae	17.3	19.9	no
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	15.7	18.0	no
Terminalia oblonga Steudel	Combretaceae	10.6	12.1	minor
Ficus boliviana L.	Moraceae	5.6	6.4	major
Schizolobium amazonicum Huber ex Ducke	Ceaesalpiniaceae	4.2	4.8	no
Maclura tinctoria (L.) D. Don ex Steudel	Moraceae	1.7	1.9	no
Sterculia sp.	Sterculiaceae	1.6	1.9	no
Hymenaea courbaril L.	Ceaesalpiniaceae	0.9	1.0	no
Caesalpinia pluviosa DC.	Ceaesalpiniaceae	0.7	0.8	minor
Pseudolmedia laevis J. F. Macbride	Moraceae	0.5	0.6	major
Anadenanthera colubrina (Vell. Conc.) Benth.	Mimosaceae	0.3	0.3	no
Tabebuia lapacho (K. Schum.) Sandwith	Bignoniaceae	0.2	0.2	no
Batocarpus amazonicum (Ducke) Fosb.	Moraceae	0.0	0.0	minor
Grand Total		87.4		
Total Food Species		17.4	19.9	
Total Major Food Species		6.1	6.9	

a = # trees extracted per 100 ha of the 2006 logging area (total area = 2445 ha); b = % extracted trees per species of total extracted in 2006.

Table 5.4. Estimated loss of food trees used by spider monkeys in La Chonta, assuming a 400 ha territory, under three different logging intensity scenarios.

	Ficus boliviana	***Pouteria nemorosa***	***Spondias mombin***	***Pseudolmedia laevis***
Diet category	*Staple*	*Late peak season*		*Fall-back/ Early peak season*
Density of trees >MCD (per ha territory)[a]	1.3	1.0	0.7	1.1
% of existing trees >MCD that were used by SM[b]	8	5	6	4
A) # trees extracted/ha in 2006[i]	0.06	0.00	0.00	0.49
Estimated proportional loss of trees[*]	4	0	0	43
B) # trees extracted/ha in 1998[ii]	0.40	0.20	0.20	0.02
Estimated proportional loss of trees[*]	32	20	28	2
C) # trees extracted/ha maximum limits[iii]	1.01	0.79	0.56	0.90
Estimated proportional loss of trees[*]	80	80	80	80

Notes: a = density of individuals above minimum cut diameter (MCD) within the spider monkey territory; b = proportion of the existing trees >MCD within the territory that were observed to be used by the spider monkeys during the study period; i = data from Agroindustría Forestal La Chonta Ltda; ii = data from Pariona (2003); iii = the Bolivian maximum legal limit is to extract 4/5 of all harvestable trees of each timber species; * estimated loss of trees from the territory, based on the extraction intensity in question, and the observed percentage of trees >MCD that spider monkeys were observed to use (fourth row in table).

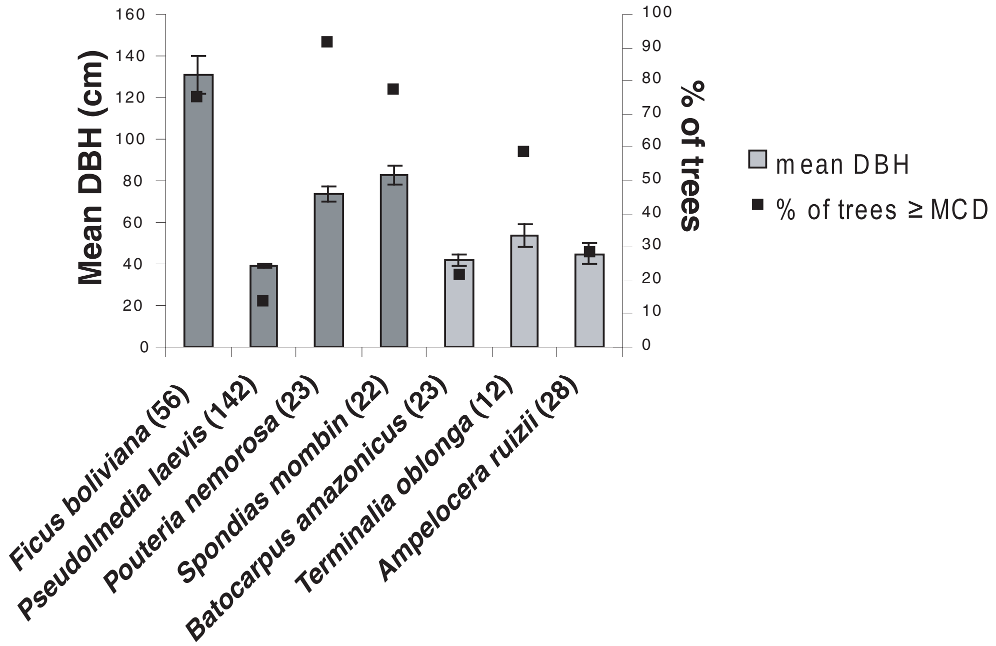

Figure 5.1. Mean (±1SE) diameter at breast height (DBH) of seven timber tree species that were observed to be used by the spider monkeys during the study period. Also indicated is the proportion of trees that were above or equal to the minimum cut diameter (MCD). The number of tree individuals used by the spider monkey community is in brackets. Dark shading = major food species (contributing >2% of total feeding time); light shading = minor food species (<2% of total feeding time).

5.5. Discussion

The primary staple food resource for this community of spider monkeys was the figs of the timber tree species *Ficus boliviana*. These figs played a major role in their diet for six of the eight months of study (Table 5.1). *Ficus boliviana* provided spider monkeys with more protein, lipids and organic material than any other plant species consumed. Figs from this species also were particularly well balanced nutritionally (Chapter 3), easily gathered by the monkeys, and readily available both spatially and temporally (Chapters 2 and 4).

In addition to comprising the staple food resource, timber tree species contributed to all of the different seasonal diets. The diet consumed at the beginning of the fruiting season was dominated by the timber tree species *Pseudolmedia laevis* and *Ficus boliviana*. At the end of the fruiting season, the timber tree species *Spondias mombin* and *Pouteria nemorosa* contributed almost 90% of spider monkeys' TNC and lipid intake. During the dry season, the spider monkeys experienced a 10-week period of relative fruit scarcity. Daily intake of TNC and lipids during this period was 50% of what the spider monkeys consumed during the late fruiting season (Chapter 4). Five timber tree species played a substantial role in the dry season diet, providing a third of their total protein intake.

Our results showed that timber tree species comprised the spider monkeys' staple food, dominated their peak season diet, and also played a significant part of their fall-back diet during the period of fruit scarcity. The spider monkeys spent 47% of their feeding time consuming food items from timber tree species. These tree species provided approximately half of the spider monkeys' total intake of macronutrients. Furthermore, spider monkeys exhibited a distinct preference for foraging within timber trees that were large enough to be eligible for harvesting.

This dominance of timber tree species in the diet and nutritional ecology may have significant repercussions. Primate population density can be strongly influenced by the abundance of staple foods (Oates 1996; Rogers et al. 2004), and fall-back foods (Weins 1977; Terborgh 1983; Marshall & Leighton 2006). It is possible that the abundance of *Ficus boliviana* contributed to the unusually large size of this spider monkey community (55 individuals, mean for *Ateles* communities is 31 individuals, Campbell in press). Furthermore, it is notable that a substantial proportion of the spider monkeys' lipid intake during the peak fruiting season was provided by timber tree species. It is likely that the spider monkeys, like other ateline primates (Peres 1994c; Di Fiore & Rodman 2001), can use the peak fruiting season to accumulate fat deposits in preparation for an upcoming period of food scarcity. Such fat reserves may be critical for survival and reproduction in this seasonal environment (Stevenson 2005).

Annual logging operations often removed timber tree species spanning all three diet categories. There were, however, large differences between years in the number of tree species harvested, due to variation in commercial demand for logs (Table 5.4). Because of inter-annual variation in demand, the resulting impact of logging on the spider monkey food resource will vary. For example, in some years, tree harvesting rates would result in the removal of a third of the staple food resource (*Ficus boliviana*), along with over 20% of the late peak season resource (*Pouteria nemorosa* and *Spondias mombin*). By contrast, in other years, few individuals of these tree species would be removed, while almost half of *Pseudolmedia laevis* trees used by spider monkeys would be taken from their territory (Table 5.4). *P. laevis* represented a substantial part of their early peak season and fall-back diets.

Logging operations thus substantially reduced the abundance of at least one of the three diet categories in a given year. For the La Chonta forestry concession, the legal logging limit does not appear to be functioning as a constraint on the number of stems cut for a given tree species. This is because the legal limit in most years appears to be well above what is taken (Table 5.4). Therefore, the impact on spider monkey communities inhabiting this concession will depend on market demand, not on the ecological roles of different tree species or the level of concern that should be associated with their removal.

Spider monkey diets are rather flexible (van Roosmalen 1985; Chapman 1987; Symington 1988c; Cant 1990; Wallace 2005) and it is possible that they can adjust to the loss of food-providing timber trees by switching to alternative food resources such as ripe fruit from non-timber species or other types of items. However, timber tree species comprised 6 of the top 10 sources of nutrients for the spider monkeys (Chapter 4). For non-timber species to compensate for this large proportion of the food resource by providing alternative fruit, they would need to do this in large quantities and at appropriate times of the year. Furthermore, there are several factors that limit the extent to which spider monkeys can switch to food items other than ripe fruit. First, their gut morphology limits how much leaf material that can be digested (small hind gut volume and fast passage rates, Milton 1981). Second, in the Neotropics, peaks in young leaf flush often occur simultaneously with peaks in ripe fruit, providing little opportunity for dietary switching (van Schaik et al. 1993). Accordingly, we observed the spider monkeys to consume young leaves mainly during the early peak fruiting season (Chapter 4). Third, when we observed the monkeys during the fruit-scarce period to switch to alternative items, these items were still predominantly sourced from *Ficus boliviana* (Table 5.2). For these reasons, it is unlikely that switching behavior sufficiently can compensate for the current rates of timber tree removal. It is also important to note that the only other common *Ficus* species in this forest which could become a potential substitute fig resource is the strangler fig *Ficus trigona*. This species also may be negatively affected by logging. Strangler fig populations can be severely depleted due to the removal of these climbers from crop trees, and the extraction of the host trees themselves (Leighton & Leighton 1983; Lambert 1991).

If the switching ability of spider monkeys is indeed limited, we would expect declines in population density after logging has reduced the abundance of important food resources. Fredericksen et al. (2007) reported that spider monkey densities were 75% lower in blocks logged one to two years previously relative to unlogged blocks in La Chonta. Similarly, population densities of other important seed dispersing vertebrate taxa, such as howler monkeys, guans (Fredericksen et al. 2007) and toucans (Felton *et al.* 2008a) also exhibited reduced population densities within areas subjected to reduced-impact logging. Declines of seed dispersers should be of concern to managers of tropical forestry concessions which depend on natural regeneration of commercial timber species (Cowlishaw & Dunbar 2000; Mason & Putz 2001). The Bolivian forestry industry is plagued by inadequate regeneration of the most important timber species, including those tree species addressed in this paper (Mostacedo & Fredericksen 1999). The documented low rates of seedling and sapling establishment may be due to damage done during extraction to advanced regeneration (Felton et al. 2006), a lack of seed trees due to past high-grading practices (Mostacedo & Fredericksen 1999), or inadequacies in silvicultural treatments (Fredericksen & Putz 2003; but see Sist & Brown 2004; Peña-Claros et al. 2007). In the long term, these problems are likely to be exacerbated by reductions in the population densities of seed dispersers.

Our results lead us to suggest that *Ficus boliviana, Spondias mombin* and *Pouteria nemorosa* are key resources for spider monkeys and that placing limits on their extraction should be considered. It is important to note that we are addressing only a single harvesting cycle in this analysis. As the current rotation period is 30 years (Peña-Claros et al. 2008) and second harvests are predicted to yield volumes only 28% of the first harvest (Dauber et al. 2005), it is likely that populations of the above mentioned tree species will be further depleted in the future. Although *Pseudolmedia laevis* was also an important food resource, we suggest that this species is of relatively low concern for spider monkey conservation. This is because it is the most common tree species in the forest, extraction rates are normally low, and spider monkeys rarely use trees of this species that are large enough to be harvested (Fig. 5.1). Because the fruiting periods of the timber species *Batocarpus amazonicus* and *Ampelocera ruizii* did not overlap with our period of data collection, the importance in our study community's diet of these spider monkey food sources (Wallace 2005; Suarez 2006) is unknown.

The findings of this study indicate that the loss of important food resources is a potentially causal factor leading to lower population densities of spider monkeys recorded in logged blocks of the La Chonta concession. We acknowledge that these conclusions are based on nutritional data from a single community of spider monkeys collected during one year. However, we believe that between-year variation in food availability is unlikely to be sufficiently large to negate the reported level of importance of timber tree species in the nutritional ecology of La Chonta's spider monkeys. Because the maintenance of seed dispersers is critical for ensuring forest recovery and regeneration (Chapman & Chapman 1996; Chapman & Onderdonk 1998), we suggest that our findings should be of significant concern to both conservationists and forest managers.

5.6. Acknowledgements

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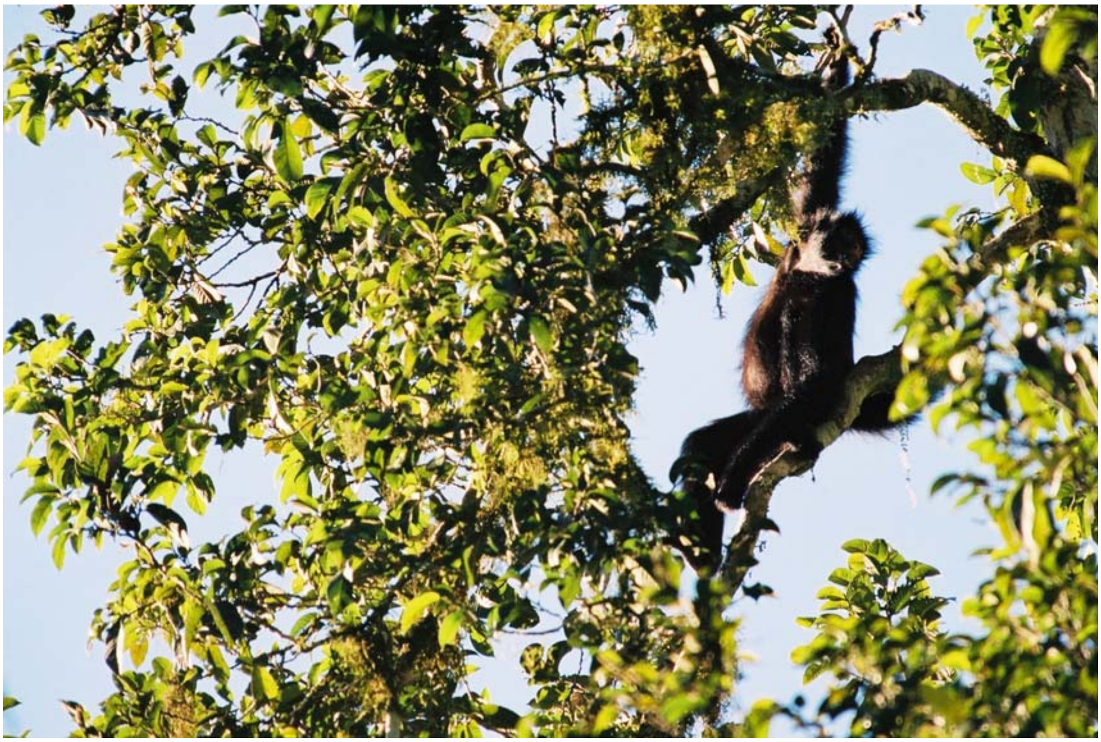

Photo byAnnika Felton

A female spider monkey sunning herself in the early morning

Chapter 6 – Conclusion

This thesis has provided new insights into spider monkey nutritional ecology with wider implications for other frugivorous primates. My research also has contributed to an improved understanding of the impacts of reduced-impact logging on the maintenance of seed dispersing animals. The aim of this concluding chapter is to provide a synthesis of the key findings from the earlier chapters. To avoid undue repetition, this chapter is presented as a short synopsis of key findings and major new insights.

6.1 The dietary pattern of this community of spider monkeys

In Chapter 2, I described the pattern of food selection in terms of the spider monkeys' feeding time budget. Descriptive approaches are a useful way of comparing the relative dominance of different food sources in the diet of different study populations. In this chapter I showed that the diet of *Ateles chamek* in La Chonta was broadly similar to other spider monkey species studied to date (Di Fiore et al. in press), consisting of a diet dominated by fruit (82% of feeding time), from a large diversity of different plant species (63 species), and exhibiting seasonal peaks in the consumption of leaves and flowers. Their diet did, however, differ from other documented spider monkey diets at a finer scale, as *Ficus* was used as a staple food source and unripe figs were a substantial part of their diet (for definitions of dietary terminology see section 1.4). Fig consumption in general comprised 45% of total feeding time. Figs were readily consumed even during times of high overall food availability. This is contrary to the general expectation that for Neotropical frugivores, *Ficus* is a fall-back food in times of fruit scarcity, rather than a staple food resource (Milton et al. 1982; Shanahan et al. 2001). The consumption of unripe figs by these so called 'ripe fruit specialists' was unusual not only because of its frequency and volume in the diet, but also because unripe figs were eaten all through the year, including periods when ripe figs and other ripe fruit were abundant. As figs were a staple food, they also played an important role in the fall-back diet consumed when ripe fruit were relatively scarce in the territory.

6.2 The process behind the pattern observed

While the dietary patterns described above were to some extent explained by an assessment of forest-wide fruit availability (Chapter 2), they were more fully explained by a thorough examination of the nutritional underpinnings of food choices. Chapter 3 provided a novel demonstration of how the nutritional strategy of a wild primate can be determined. By applying the Geometric Framework for nutrition, I was able to show that the pattern of nutrient intake was explained by protein-dominated macro-nutrient balancing, rather than energy or protein maximization, or avoidance of plant secondary metabolites. I show that protein intake by spider monkeys mimicked that of humans (Simpson & Raubenheimer 2005): protein was regulated more tightly than carbohydrates or fats, and disproportionately influenced total energy intake. This finding, supported by further analysis presented in Chapter 4, has far-ranging implications, spanning the fields of primate nutritional ecology, evolutionary theory and management of wild and captive primate populations.

My finding in Chapter 3, that nutrient balancing was the primary goal of nutrient intake by this spider monkey community, contrasts with the theory that foraging decisions of ripe fruit specialists are largely dictated by their attempts to maximise energy intake (Rosenberger & Strier 1989; Strier 1992; Di Fiore & Rodman 2001). This perception is primarily based on observations from the wild that spider monkeys sometimes (but not consistently) preferentially select energy-dense food items, especially those that are rich in lipids (Castellanos 1995; Dew 2005; Di Fiore et al. in press). My research emphasizes the difficulty of inferring underlying nutritional goals from observational data that does not take daily nutrient intake into account. Although spider monkeys may consume lipid-rich foods disproportionately to their abundance (thus expressing a "preference", Krebs 1989), this does not necessarily indicate that lipids or total energy are the primary drivers behind feeding choices.

Geometric analysis revealed that protein intake remained stable throughout the year and was not altered by the presence or absence of leaves in the diet. This is notable, because it is often stated that frugivorous primates must include leaves in their diet in order to obtain sufficient protein (Milton 1981; Oftedal 1991; Milton 1993a; Chapman & Russo 2007; Lambert 2007; Strier 2007). My results show that this is not the case for spider monkeys, at least on a daily basis, as protein intake targets could be achieved with a diet comprised solely of ripe fruit during the periods of highest ripe fruit availability.

Fluctuations in habitat-wide fruit availability did however significantly influence which strategy the spider monkeys would employ on a daily basis to reach their nutritional requirements. In Chapter 4, I show that individuals would reach their daily end point in nutritional space (balance between protein and non-protein energy intake) by either: (*a*) consuming nutritionally-balanced foods, (*b*) alternating between nutritionally complementary foods, or (*c*) ingesting large amounts of energy-dense fruit and thereby consuming "surplus" energy (more than is needed for maintenance of body weight, Knott 1998)). Individuals were more likely to concentrate on nutritionally-balanced foods (option *a*) when ripe figs were abundant in the habitat and figs constituted a large proportion of their daily diet. In contrast, individuals were more likely to mix complementary foods on a daily basis (option *b*) when both ripe figs and other ripe fruit were available in low to moderate abundances, e.g. during the fruit scarce period. Finally, they were more likely to ingest extremely large amounts of non-protein energy (option *c*) when figs were scarce but other ripe fruit were abundant.

Spider monkeys reached their daily protein target on a 100% fruit diet during the peak fruiting season because of their ability to ingest surplus non-protein energy from fruit extremely rich in soluble carbohydrates and lipids (Chapter 4). The data presented in Chapter 3 shows large variations in the daily intake of non-protein energy over the course of the year. It is likely that spider monkeys take advantage of the increased availability of energy-dense food during the peak fruiting season by consuming more energy than is necessary for basic maintenance, and converting this into fat deposits in preparation for the upcoming annual period of food scarcity when energy intake halved (Chapter 4).

The propensity of spider monkeys to ingest surplus energy in the quest to reach a daily protein target is relevant to humans. While occasional deposition of extra fat reserves is a beneficial trait for monkeys inhabiting a forest with highly fluctuating food availability, the same can not be said for humans living in affluent societies. Human obesity is one of the most pressing health problems in Western countries. The modern obesity epidemic has been attributed to a mismatch between modern diets and phenotypes that evolved in Paleolithic nutritional environments. Notably, the similarities between *Homo* and *Ateles* demonstrated in Chapter 3 indicate that the origins of human susceptibility to obesity may date before the previously speculated Paleolithic era.

The knowledge gained in Chapters 3 and 4 are also relevant to the management of captive primates and for the management of forests. I describe these two conservation-related implications in section 6.4.

6.3 Why was *Ficus* a dominant food resource?

My research indicates that there are several reasons why figs played a large role in the diet of the spider monkey community. First, the most commonly eaten fig species, *Ficus boliviana*[1] and *F. trigona*, were relatively common and their large fruit crops were available for eight to nine months of the year (Chapter 2). Second, the geometric analysis suggested that several species of ripe figs (*Ficus boliviana* included) possessed a macro-nutrient balance similar to the mean observed intake trajectory of the spider monkeys (Chapter 3). Most other ripe fruit were not as “well balanced” as these ripe figs, having higher concentrations of soluble carbohydrates and/or lipids (Chapter 4). Third, figs contained high concentrations of inorganic material, and provided individuals with 44% of their intake of inorganic material. I make the reasonable assumption that a large proportion of the inorganic material consisted of minerals (as opposed to silica), as figs are known to be extremely rich sources of bio-available calcium and other essential minerals critical for maintenance and reproduction in animals (Duhan et al. 1992; O'Brien et al. 1998; Ruby et al. 2000; Wendeln et al. 2000). In addition, I found that the unripe figs consumed by spider monkeys constituted an easily harvestable, nutritionally rewarding,

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[1]. The taxonomy of this species is uncertain at the time of printing. This species may be *Ficus insipida* (synonym *F. glabrata*), but because the name *F. boliviana* is the accepted classification employed by Bolivian researchers I have chosen to use it throughout the thesis. Please contact the author for updated nomenclature.

complementary food (Chapter 4). An added benefit of unripe figs was that they were continuously available in the territory in contrast to ripe figs. Notably, the period of ripe fig scarcity partially overlapped with the period of general fruit scarcity, thus making unripe figs a valuable alternative food resource (Chapter 2).

I suggest that these factors collectively have contributed to figs being the staple food of spider monkeys in La Chonta. The importance of figs is emphasized by a further analysis presented in Chapter 4, where I show that the spider monkeys included a large number of other ripe fruit types in their diet only when ripe figs were scarce, despite the opportunity to do otherwise. There is a common perception that figs are a critical fall-back food for tropical frugivores, but generally not preferred when other options are available (Milton et al. 1982; Shanahan et al. 2001). Contrary to this view, my results indicate that the consumption of a variety of different fruits was used as a strategy for overcoming periods of fig scarcity. I tentatively suggest that the unusually large size of this spider monkey community (55 individuals) may be at least partially attributable to having ready access to this nutritionally-balanced and mineral-rich staple food.

6.4 Implications of this study to conservation and management

6.4.1 Relevance to certified selective forestry

The catalyst for this project was my aim to contribute to the understanding of the impacts of forestry practices on primates. Tropical forestry concessions are often reliant on natural regeneration and are therefore dependent on the maintenance of seed dispersers, such as spider monkeys (Cowlishaw & Dunbar 2000; Mason & Putz 2001). Spider monkeys belong to a group of primates that are highly sensitive to human disturbances such as the selective harvesting of timber, due to their slow reproductive rate, large body size and reliance on ripe fruit (Skorupa 1986; Johns & Skorupa 1987; Peres 1994b; Sorensen & Fedigan 2000). For these reasons, I quantified the importance of timber tree species as food resources for these important seed dispersers.

Surveys conducted previously in the certified forestry concession La Chonta, Bolivia, showed that forest that had been logged one and two years previously sustained only 25% of population densities found in comparable unlogged sections (Fredericksen et al. 2007). This significant difference in spider monkey density occurred despite the fact that reduced-impact logging techniques had been employed. Harvesting of timber trees which provide important food resources for spider monkeys may substantially contribute to this reported reduction in population density (Chapter 5). My study community, which occupied an unlogged section of the concession, spent 47% of their feeding time consuming items from timber tree species. Timber trees provided approximately half of their total intake of non-structural carbohydrates, lipids and available protein. Furthermore, spider monkeys exhibited a distinct preference for foraging within individuals of timber tree species that were large enough to be eligible for harvesting. Most importantly, these tree species comprised their staple food, dominated their peak season diet, and also played a significant part of their fall-back diet.

Specifically, I single out three key timber tree species as being key resources for spider monkeys. The timber tree species *Ficus boliviana* played a major role in spider monkey diets for six of the eight months of detailed data collection. This tree species provided spider monkeys with more protein, lipids and minerals than any other plant species consumed in this study (ranging from 25%-34% of total intake). During the late peak fruiting season individuals presumably accumulated fat before the long annual period of fruit scarcity. During this period, two timber tree species that produce energy-dense fruit, *Spondias mombin* and *Pouteria nemorosa,* contributed almost 90% of spider monkeys' non-protein energy, and 50% of their protein.

Although there are large differences between years in the commercial demand for timber from different tree species, I estimated that under current timber extraction intensities, spider monkeys in this forest lose a significant proportion of their food sources (Chapter 5). I suggest that for territorial non-volant animals like spider monkeys, the most efficient means by which their populations can be secured, and thereby their ecological services maintained, would be to limit the harvesting of timber tree species that function as important food sources; in this case *Ficus boliviana, Spondias mombin* and *Pouteria nemorosa*. Such limitations may also benefit other important seed dispersers, such as howler monkeys, guans, and toucans, which also decline in densities after reduced-impact logging has affected their habitat (Fredericksen *et al.* 2007; Felton *et al.* 2008a). Suggested adjustments to harvesting procedures should benefit the forestry industry through improved tree regeneration.

6.4.2 Relevance to forest restoration

The results from this study suggest that an understanding of the relative value of different food sources is important for making decisions aimed at maintaining populations of primates. For example, nutritionally-balanced food sources that are used extensively by a wild population may need special attention in conservation planning, for example as target tree species for establishment in vegetation restoration. My results also suggest that certain peak-season fruit sources may be critical for the storage of fat which individuals rely upon during periods of food scarcity. These benefits are often overlooked when practitioners concentrate on resources used by animals during periods of food scarcity, e.g. keystone resources or fall-back foods (see section 1.4 for definitions of these terms). I suggest that plant species that provide energy-dense fruit and supply an energy surplus during the peak fruiting season should also be given special attention in conservation planning. Indeed, a complex picture emerges from my geometric analysis, in which the monkeys reach their nutritional requirements through selecting complementary combinations of foods. A conservation challenge therefore is to conserve or supply a diversity of foods which provide the primates with access to the optimal region within nutrient space (see also Milton 1982). This is certainly not an easy endeavour, as informed decisions require detailed information on the nutrient intake of the primate in question and relevant chemical analyses of the foods consumed. However, studies such as this one may be of use as an indicator of the types of processes that may be driving or can ameliorate population declines.

6.4.3 Relevance to captive management

The geometric analysis presented in Chapter 3 showed that spider monkeys would ingest large amounts of carbohydrates and lipids in order to reach their protein target when their diet was imbalanced. This energy surplus was likely to be stored as fat and used during subsequent leaner periods. Primates that have evolved in environments with significant annual or supra-annual fluctuations in food availability appear to be especially capable of storing excess energy as fat (Leighton 1993; Knott 1998; Di Fiore & Rodman 2001; Schwitzer & Kaumanns 2001), especially when they are kept in captivity (Jones 1982; Schwitzer & Kaumanns 2001). In fact, obesity and associated health problems in captive primates is a common problem (Jones 1982; Terranova & Coffman 1997; Videan *et al.* 2007). The findings of my study suggest that an adjustment of the macro-nutritional balance of primate diets might be an option for mitigating the problem of obesity in captivity. While species-specific data such as mine are hard to gather, managers of captive populations should consider these general findings when trying to improve the nutritional state of obese primates in captivity.

6.5 Other lessons from this study

The methodology I used in this research differed in three important ways from the majority of studies addressing primate nutritional ecology. These differences involved (i) techniques by which data was collected in the field; (ii) analytical methods employed in the laboratory; and (iii) means by which I analysed the resultant data. Several benefits arise from these approaches.

The common method of collecting data on spider monkey behaviour is to use point scan sampling which involves periodic scans conducted on alternate individuals throughout the day (Altmann 1974; Dunbar 1976). The alternative method - continuous all-day data collection of the same focal individual - is generally discouraged because individual spider monkeys are difficult to follow throughout an entire day. This is because of the difficulty of identifying individuals (especially species with all-black coloration, such as *Ateles chamek*), the fluidity of subgroups, and their rapid movements through the dense rainforest canopy high above the observer. I found that, despite these challenges, continuous all-day follows of focal animals were valuable as this was the only way I could properly address my research questions. Only by analysing complete days of feeding data was I able to reach the majority of the conclusions of this thesis.

In the laboratory I was able to conduct an *in vitro* digestion assay of spider monkey food. This analysis allowed me to estimate the proportion of total nitrogen available to the consumer versus how much was bound up by dietary tannins. Thus, I was able to calculate the amount of “available protein” (total available nitrogen x 6.25) ingested by the spider monkeys, and contrast that with the amount of “crude protein” ingested (total nitrogen x 6.25). While no *in vitro* digestibility procedure can perfectly represent the complexity of *in vivo* processes, it does allow for a more realistic assessment of how much of the dietary protein can be absorbed by an animal. In many primate studies, crude protein is the only reported protein fraction and conclusions are based on the patterns observed in crude protein concentrations in foods and associated intakes by the animals. My results highlighted the need for taking digestion-inhibiting agents into account when assessing protein intake. For example, although the concentration of crude protein was higher in ripe than immature figs of *Ficus boliviana*, I found that the opposite was true for available protein. This helped me to explain why unripe figs were a preferred food item (Chapter 4). Furthermore, I found that the proportion of the daily diet comprised of available protein remained steady across all three phenological seasons, while the amount of crude protein fluctuated by 75%. This directly influenced my ability to accurately analyse the nutritional strategy of these spider monkeys (Chapter 3). It would not have been possible to identify a clear pattern of protein-dominated macro-nutrient balancing if I had used crude protein intake as the unit of analysis.

The application of the Geometric Framework (GF) to my nutrient intake data was another novel and valuable approach taken in this investigation. This multi-dimensional analytical technique has, to the best of my knowledge, not previously been used in the field of primatology. The GF has, however, successfully been used for a variety of other vertebrate and invertebrate taxa (Chambers *et al.* 1995; Simpson & Raubenheimer 2001;2005; Raubenheimer & Simpson 2006; Robbins *et al.* 2007; Ruohonen *et al.* 2007). Conventional tabulatory approaches are useful in describing and comparing primate diets and for elucidating the relative importance of different food species. The application of the GF was a valuable complement to these conventional approaches as it allowed me to understand the nutritional underpinnings of diet selection. A principle benefit of the GF is that data can be analysed without any preconceived assumptions of what the primary driver of nutrient intake may be. Evidence for any possible primary driver can be found by using the GF: energy maximization, protein maximization, avoidance of plant secondary metabolites, nutrient-balancing or any other possibility. The associated lack of an *a priori* assumption provides the researcher with greater objectivity when assessing the underlying nutritional goals of their species of interest.

6.6 Limitations of this study

I am aware of several limitations of this study. The conclusions from this thesis are based on data obtained from the observations of a single spider monkey community. For logistical limitations, no replication at the community level or forest-type level was possible. Whether my results are representative of other spider monkey communities inhabiting La Chonta or other semi-deciduous moist forests in the Neotropics remains to be shown by future research. The dietary data span a relatively short period of time: February to September 2004. It therefore does not incorporate between-year differences in fruiting phenology, and associated diets. Information regarding nutrient concentrations of different food items is based on small sub-samples of the food actually consumed. To incorporate as much between-tree and between-season variation in nutrient content as possible, I collected food samples from multiple feeding trees spanning their entire fruiting period(s), and combined samples of the same species/food type before conducting chemical analysis.

It is unlikely that my conclusions regarding the nutritional strategy of the spider monkeys would be altered by a longer field period or larger food sample sizes. I also feel confident in concluding that *Ficus* was a staple food resource for this community of spider monkeys. Fig trees comprised the majority of the trees used by spider monkeys throughout the entire habituation period. Finally, I believe that the general conclusion regarding the level of importance of timber tree species in the spider monkey diet would not be negated by interannual differences in food availability or larger sample sizes.

6.7 Key areas for future work

The following are key areas for future research that relate to issues raised in this thesis:

- Research is needed to determine whether protein-dominated macro-nutrient balancing is the primary driver of diet selection in other spider monkey species inhabiting other forest types. Similar investigations into nutritional strategies of wild non-human primates representing a wide range of diets and phylogenetic relatedness to humans would also be of value to the field of primate nutritional ecology and evolutionary theory.
- Research is needed to compare the nutritional composition of figs abundant in other spider monkey study areas, and determine whether their macro-nutritional balance in relation to the monkeys' preferred intake trajectory can explain why figs are important food sources for some populations, but not for others.
- Research is needed to directly quantify the impact of reduced-impact logging on spider monkey populations. A replicated 'before-and-after' design where the researcher can control the amount of food trees that are removed, would be valuable in elucidating short- and long-term impacts. Although such an empirical study would be difficult to perform, it would contribute with quantifiable limits regarding appropriate harvesting levels for particular timber tree species.

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Photo by Annika Felton

A female spider monkey resting on a sunny branch of *Pseudolmedia laevis* together with her infant daughter, while grooming her adult son.

Appendix 1: List of all food sources of *Ateles chamek* in La Chonta.

The table shows % time spent feeding over the year from different pheno-phases. Full and partial follow days included.

Family	Scientific name	Cat.[a]	% time[b]	Rank[c]	R%	U%	YL%	L%	F%	OV%	I %	Month[d]
TOTAL FOR STUDY:					59.1	23.0	10.1	2.9	4.7	0.2	0.1	
AMARANTHACEAE	*Chamissoa* sp.1	**L**	*	52-66	x							-
ANACARDIACEAE	*Spondias mombin* L.	**T**	1.94	11	1.94							3-4
ANNONACEAE	*Rollinia herzogii* R. E. Fries	T	0.08*	34-35	0.08							-
ARACEAE	*Monstera sp.*	E	0.03	41-42						0.03		-
ARALIACEAE	*Dendropanax arboreus* (L.) D. & P.	**T**	2.32	8	2.32							7-8
ARALIACEAE	*Didymopanax morototoni* Decne. & Planch.	**T**	0.13	27-29	0.13							8
ARECACEAE	*Astrocaryum murumuru* C. Martius	**P**	0.49	20	0.49							3-5
ARECACEAE	*Attalea phalerata* Mart. ex Spreng.	**P**	0.22	24	0.11					0.11		10
ARECACEAE	*Bactris gasipaes* Kunth.	**P**	0.01	45-49					0.01			-
ARECACEAE	*Socratea exorrhiza* H. A. Wendl.	**P**	0.57	19	0.57							cont.
ARECACEAE	*Syagrus sancona* Karsten	**P**	0.09	30-33					0.09			8-2
ASCLEPIADACEAE	*Marsdenia macrophylla* E. Fourn	L	0.15	26				0.15				-
BIGNONIACEAE	*Arrabidaea verrucosa* (Standl.) A.H. Gentry.	**L**	*	52-66			x					spor.
BIGNONIACEAE	*Clytostoma uleanum* Kraenzl.	**L**	0.05	37					0.05			0
BIGNONIACEAE	*Melloa quadrivalvis* (Jacq.) A.H. Gentry	**L**	0.93	16			0.80	0.14				0
BIGNONIACEAE	*Tabebuia serratifolia* (Vahl) G. Nicholson	**T**	*	52-66				x				0
BIGNONIACEAE	*Tanaecium nocturnum* Bureau & K. Schum.	**L**	0.02	43-44				0.02				0
BORAGINACEAE	*Cordia alliodora* (Ruiz & Pavón) Oken	**T**	*	52-66	x							11-12
CAESALPINIACEAE	*Caesalpinia pluviosa* DC.	T	0.01	45-49			0.01					-
CARICACEAE	*Jacaratia spinosa* (Aubl.) A. DC.	**T**	1.27	14	0.60	0.11	0.04	0.17	0.35	0.01		11-5
CECROPIACEAE	*Cecropia concolor* Willd.	**T**	0.02*	43-44	0.02							2-4 7-8
CHRYSOBALANACEAE	*Hirtella triandra* Sw.	T	0.09	30-33	0.09							-
COMBRETACEAE	*Terminalia oblonga* (Ruiz & Pavón) Steudel	T	0.09	30-33			0.08	0.00				-

Cont. Appendix 1

Family	**Scientific name**	**Cat.[a]**	**% time[b]**	**Rank[c]**	**R%**	**U%**	**YL%**	**L%**	**F%**	**OV%**	**I %**	**Month[d]**
CONVOLVULACEAE	*Merremia cf. ternifolia* Pittier.	L	0.01	45-49			0.01					-
DIOSCOREACEAE	*Dioscorea anthogene*	L	0.09	30-33	0.05		0.02	0.02				-
EUPHORBIACEAE	*Hura crepitans* L.	**T**	*	52-66		x						cont.
EUPHORBIACEAE	*Sapium glandulosum* (L.) Morong	**T**	1.46	12	1.44	0.02						2-3
FABACEAE	*Machaerium oblongifolium* Vogel	**L**	1.05	15			1.05					0
LECYTHIDACEAE	*Cariniana ianeirensis* R. Knuth	T	*	52-66		X						-
MALVACEAE	*Ceiba pentandra* (L.) P. Gaertner	**T**	0.20	25			0.20					0
MALVACEAE	*Ceiba speciosa* St. Hilaire	**T**	<0.01	50-51			0.00					5-10
MELIACEAE	*Guarea guidonia* (L.) Sleumer	T	*	52-66	x							-
MIMOSACEAE	*Inga edulis* Mart.	**T**	1.35	13	1.35							2-4
MORACEAE	*Batocarpus amazonicus* (Ducke) Fosb.	**T**	2.28	9	x		2.26	0.01				11
MORACEAE	*Brosimium guadichaudii* Trécul	**T**	0.04	38-40			0.04					10-11
MORACEAE	*Ficus boliviana* C.C. Berg	**T**	28.59	1	8.56	15.6	4.38	0.01		0.00		spor.
MORACEAE	*Ficus eximia* Schott	**T**	0.45	21	0.31	0.14				0.00		-
MORACEAE	*Ficus gomelleira* Kunth & Bouché	**T**	0.04*	38-40		0.04						-
MORACEAE	*Ficus pertusa* L. f.	**T**	0.13	27-29	0.11	0.02						spor.
MORACEAE	*Ficus sp.*	**T**	*	52-66	x							0
MORACEAE	*Ficus trigona* L. f.	**T**	20.31	2	17.8	2.00	0.47					spor.
MORACEAE	*Pseudolmedia laevis* J. F. Macbride	**T**	9.36	4	2.98	2.23	0.12	0.01	4.02			8-11
MYRISTICACEAE	*Virola sebifera* Aublet	**T**	0.44	22	0.44							5, 8
MYRTACEAE	*Myrciaria* sp.	**T**	10.30	3	10.3							2-8
NYCTAGINACEAE	*Neea cf. steimbachii* Heimerl	T	*	52-66			x					-
QUIINACEAE	*Quiina florida* Tul.	**T**	*	52-66	x							0
RUBIACEAE	*Alibertia verrucosa* S. Moore	**T**	0.03	41-42	0.03							10-2
RUBIACEAE	*Calycophyllum spruceanum* (Benth.)	T	*	52-66						x		-
RUTACEAE	*Zanthoxylon rhoifolium* Lam.	T	0.01	45-49		0.01						-
SAPINDACEAE	*Paullinia elegans* Cambess.	**L**	0.59	18	0.59							3-4
SAPINDACEAE	*Talisia esculenta* (Cambess.) Radlk.	T	0.04	38-40	0.04							-
SAPOTACEAE	*Pouteria macrophylla* (Lam.) Eyma	**T**	*	52-66	x							3, 8, 12
SAPOTACEAE	*Pouteria nemorosa* Baehni	**T**	4.08	5	1.31	2.73				0.05		2-3

Cont. Appendix 1

Family	**Scientific name**	**Cat.**[a]	**% time**[b]	**Rank**[c]	**R%**	**U%**	**YL%**	**L%**	**F%**	**OV%**	**I %**	**Month**[d]
STERCULIACEAE	*Guazuma ulmifolia* Lam.	**T**	3.57	7	3.57							6-10
STYRACACEAE	*Styrax tessmannii* Perkins	**T**	*	52-66	x							5, 8
TILIACEAE	*Heliocarpus americanus* L.	T	2.16	10			0.15	2.02				-
ULMACEAE	*Ampelocera ruizii* Klotzsch	**T**	0.30	23			0.16	0.03	0.11			10-12
ULMACEAE	*Celtis iguanea* (Jacq.) Sarg.	**L**	3.84	6	3.84							3-6
URTICACEAE	*Urera baccifera* (L.) Gaudich.	T	0.13	27-29			0.03	0.10				-
VITACEAE	*Vitaceae sp. 1*	**L**	0.01	45-49						0.01		12
	unidentified plant (1 sp)	T	<0.01	50-51				0.00				
	unidentified lianas (4 spp)	**L**	0.65	17		0.02	0.27	0.24	0.12			
	unidentified insect	I	0.08	34-35							0.08	
	unidentified epiphyte (1 sp)	E	*	52-66	x							
	unid. caterpillars in *Terminalia oblonga*	I	*	52-66							x	
	unid. arboreal termite mound	I	0.06	36							0.06	

Appendix 2: Nutritional contents of food items consumed by *Ateles chamek* in La Chonta.

Items are listed in order of family. Seeds in fruit were not included in the nutritional analysis.

Species name	Family	Type	% BA	% T	% H_20	% ash	% CP	% AP	% TNC	% lip	% NDF	% DMD	P: (TNC+L)	n
Spondias mombin	Anacardiaceae	R	1.5	1.69	83	5.2	3.3	1.3	57.2	2.5	9.9	80	0.03	2
Rollinia herzogii	Annonaceae	R	<0.01	*	61	6.9	7.2	3.6	24.7	2.3	55.2	46	0.17	1
Dendropanax arboreus	Araliaceae	R	1.4	2.69	58	1.2	**5.4**	**3.0**	10.6	21.8	53.5	28	0.07	1
Didymopanax morototoni	Araliaceae	R	0.1	0.13	65	2.5	6.2	6.8	19.4	33.2	14.5	50	0.10	2
Astrocarium murumuru	Arecaceae	R	0.7	0.64	68	4.4	3.0	2.4	58.1	3.4	20.9	72	0.05	3
Socratea exhorriza	Arecaceae	R	7.0	0.66	85	4.1	6.8	3.1	35.9	0.4	42.3	70	0.12	1
Syagrus sancona	Arecaceae	F	0.02	0.11	95	7.5	15.0	4.7	32.0	3.6	55.3	**57**	0.17	2
Marsdenia macrophylla	Asclepiadaceae	L	-	0.19	76	14.5	14.0	10.1	8.4	5.0	50.6	**84**	0.73	2
Melloa quadrivalvis	Bignoniaceae	L	-	0.08	64	8.0	19.2	14.3	3.3	2.5	67.8	42	2.25	1
Melloa quadrivalvis	Bignoniaceae	YL	-	0.93	79	7.1	28.0	25.8	8.0	3.0	38.7	76	2.47	3
Cordia alliodora	Boraginaceae	R	1.3	*	66	5.0	3.8	1.8	67.4	1.3	26.8	98	0.04	1
Jacaratia spinosa	Caricaceae	R	0.8	0.87	82	3.7	7.8	6.1	64.4	1.7	18.6	113	0.13	4
Jacaratia spinosa	Caricaceae	L	0.8	0.12	77	11.9	14.5	6.1	9.8	4.4	65.1	**51**	0.44	1
Jacaratia spinosa	Caricaceae	YL	0.8	*	83	8.8	18.2	6.5	7.4	4.2	59.1	57	0.56	1
Jacaratia spinosa	Caricaceae	FLB	0.8	0.43	85	10.8	19.1	9.7	7.6	4.5	55.8	70	0.77	1

Cont. Appendix 2

Species name (#)	**Family**	**Type**	**% BA**	**% T**	**% $H_2$0**	**% ash**	**% CP**	**% AP**	**% TNC**	**% lip**	**% NDF**	**% DMD**	**P: (TNC+L)**	**n**
Cecropia concolor	Cecropiaceae	R	0.03	*	62	12.6	11.0	6.4	17.3	7.0	59.2	**70**	0.27	3
Hura crepitans	Euphorbiaceae	I	8.6	*	-	7.8	11.9	6.6	19.8	1.7	28.8	78	0.40	1
Sapium glandulosum	Euphorbiaceae	R	0.8	0.73	18	2.0	8.7	12.1	19.7	34.4	0.0	54	0.18	1
Machaerium oblongifolium	Fabaceae	YL	-	1.29	79	5.8	19.1	13.5	7.2	5.4	74.9	71	0.99	4
Inga edulis	Leguminosae	R	0.4	1.17	73	1.8	4.2	3.8	72.3	0.8	13.0	114	0.07	3
Inga edulis	Leguminosae	MR	0.4	*	-	3.7	9.7	6.2	35.9	1.9	52.1	**83**	0.22	4
Ceiba pentandra	Malvaceae	YL	0.2	0.26	74	11.8	23.8	15.4	6.7	5.6	67.5	66	1.14	1
Batocarpus amazonicus	Moraceae	R	0.2	*	70	4.8	4.6	4.0	65.6	2.9	12.9	98	0.08	1
Batocarpus amazonicus	Moraceae	LB/YL	0.2	2.64	77	8.9	**16.5**	**5.6**	10.4	3.8	63.3	57	0.42	2
Brosimum guadichaudii	Moraceae	R	0.2	*	71	4.4	7.0	4.7	56.3	1.6	25.6	104	0.11	4
Brosimum guadichaudii	Moraceae	L	0.2	0.05	73	8.5	12.4	4.8	11.2	3.6	56.6	45	0.35	2
Ficus boliviana	Moraceae	I (1)	6.9	9.02	70	10.8	**6.5**	**4.3**	9.9	3.3	50.5*	**53**	0.35	2
Ficus boliviana	Moraceae	R (0.3)	6.9	7.51	55	7.9	**8.1**	**2.2**	24.0	2.7	41.6*	**54**	0.11	5
Ficus boliviana	Moraceae	L	6.9	0.01	72	14.4	9.7	2.6	20.1	7.1	51.4	39	0.10	1
Ficus boliviana	Moraceae	LB	6.9	5.26	67	11.1	**15.6**	**9.2**	7.2	3.6	52.1	65	0.85	3
Ficus boliviana	Moraceae	YL	6.9	0.13	62	11.0	16.2	8.0	6.4	3.3	55.0	63	0.81	2
Ficus boliviana	Moraceae	EB	6.9	4.09	76	11.2	**16.2**	**5.3**	4.8	3.0	*	69	0.66	3
Ficus pertusa	Moraceae	R (1)	0.8	0.15	75	8.5	5.8	2.4	38.8	1.9	*	66	0.08	2
Ficus eximia	Moraceae	R (1)	<0.01	0.23	71	10.4	1.3	2.6	53.1	2.6	*	69	0.06	1
Ficus sp.	Moraceae	R 1	0.01	*	86	10.2	2.8	8.1	5.4	3.0	*	74	0.95	1
Ficus trigona	Moraceae	R (0)	7.0	18.54	82	6.5	**4.1**	**0.9**	24.8	2.2	*	54	0.04	9

Cont. Appendix 2

Species name	**Family**	**Type**	**% BA**	**% T**	**% $H_2$0**	**% ash**	**% CP**	**% AP**	**% TNC**	**% lip**	**% NDF**	**% DMD**	**P: (TNC+L)**	**n**
Ficus trigona	Moraceae	I (1)	7.0	1.00	82	9.8	5.5	1.8	11.5	3.4	*	41	0.13	8
Pseudolmedia laevis	Moraceae	R	9.8	2.77	77	3.5	**5.2**	**2.6**	69.0	0.9	17.4	102	0.05	2
Pseudolmedia laevis	Moraceae	MR	9.8	1.30	78	4.6	7.1	3.0	48.4	1.9	34.7	103	0.08	1
Pseudolmedia laevis	Moraceae	FLB	9.8	5.18	65	10.6	**10.0**	**3.6**	14.7	3.2	51.8	53	0.23	3
Pseudolmedia laevis	Moraceae	I	9.8	1.08	86	7.0	10.4	3.5	12.1	3.2	47.2	**73**	0.26	4
Pseudolmedia laevis	Moraceae	IB	9.8	0.09	67	7.0	11.0	2.4	10.0	4.3	67.3	**56**	0.18	1
Virola sebifera	Myristicaceae	R	0.01	0.59	34	0.0	2.7	3.0	40.6	22.1	8.8	56	0.05	1
Myrciaria sp.	Myrtaceae	R	0.7	9.95	70	4.0	**3.1**	**1.0**	35.4	0.6	30.6	66	0.04	3
Myrciaria sp.	Myrtaceae	MR	0.7	0.72	70	4.5	4.2	1.1	41.0	0.4	25.3	**65**	0.04	1
Quiina florida	Quiinaceae	R	0.01	0.05	60	2.1	2.9	1.0	49.1	2.0	38.8	97	0.03	1
Paullinia elegans	Sapindaceae	R	-	0.64	46	1.5	2.2	1.4	32.0	1.4	13.7	92	0.06	5
Pouteria nemorosa	Sapotaceae	I	2.6	0.66	90	4.1	2.6	2.0	63.0	3.7	5.8	113	0.04	1
Pouteria nemorosa	Sapotaceae	R/MR	2.6	2.41	94	8.7	**3.2**	**1.8**	39.2	4.4	9.9	100	0.05	7
Guazuma ulmifolia	Sterculiaceae	R	0.6	3.44	35	2.7	**4.4**	**1.7**	25.8	1.1	57.7	50	0.09	2
Heliocarpus americanus	Tiliaceae	L	0.2	2.01	73	11.3	**16.2**	**7.1**	10.3	4.9	65.5	51	0.48	6
Heliocarpus americanus	Tiliaceae	YL	0.2	0.06	76	11.7	19.0	9.5	8.7	5.0	70.1	53	0.68	1
Ampelocera ruizii	Ulmaceae	YL	6.9	0.22	77	10.9	23.4	22.3	6.3	3.1	48.9	89	2.38	5

Cont. Appendix 2

Species name	Family	Type	% BA	% T	% H_20	% ash	% CP	% AP	% TNC	% lip	% NDF	% DMD	P: (TNC+L)	n
Celtis iguanea	Ulmaceae	R	-	1.69	48	5.8	7.8	7.1	71.2	0.0	2.6	96	0.14	2
Urera baccifera	Urticacaeae	L	2.0	0.13	69	15.2	17.0	10.4	5.1	3.0	59.3	63	1.25	1
Vitaceae sp. 1	Vitaceae	AR	-	0.01	86	11.3	10.3	7.5	7.7	5.9	56.4	80	0.50	1
caterpillar**		A		*	86	12.9	30.5	27.8	1.8	3.5	60.2	94	4.09	1
unid epiphyte		S		*	93	13.3	3.5	3.2	27.5	2.1	34.2	100	0.14	1
minimum			0.01		18	0.0	1.3	0.9	1.8	0.0	0.0	28.4	0.03	
average			3.15		71	7.6	10.2	6.2	26.9	4.7	41.1	71.3	0.47	
maximum			9.75		95	15.2	30.5	27.8	72.3	34.4	74.9	114	4.09	

Column headings: Type: EB = whole emerging fruit bud; I = whole immature fruit; MR = pulp of medium ripe fruit; R = pulp of ripe fruit (and aril if present); F = whole flower; FLB = whole flower bud; LB = whole leaf bud; YL = whole young leaf; L = mature leaf exl petiole; AR = aerial root; A = animal matter; S = stalk; % BA: Species specific percentage of estimated total basal area (m^2/ha) of trees DBH > 10cm (Chapter 2). For members of Arecaceae % of total density (trees/ha) is presented. (-) no basal area or density information available for lianas; % time: percentage of the total feeding time recorded for focal animals during full day follows (51 days). (*) feeding time not quantified; %H_2O = proportion of fresh weight made up by water; CP = crude protein (tot N x 6.25); AP = available protein estimated from *in vitro* assay (available N x 6.25); TNC = total non-structural carbohydrates (water-soluble carbohydrates + starch); lip = lipids; NDF = neutral detergent fiber; P:(TNC+L) = ratio between protein and non-protein energy (TNC+Lipids); % DMD = measure of dry matter digestibility (see Methods), % DMD = 100 indicates 100% digestibility of total dry matter; n = number of individual plants sourced for samples. In many cases several samples were taken from the same plant individual at different occasions; Notes: * NDF values of fig pulp may have been overestimated by the NIRS and are therefore not displayed. **Nutritional values of caterpillars should be interpreted with caution. Because this was the only sample consisting of animal material NIRS may not have been able to accurately predict levels of chemical attributes.

Appendix 3: Proportion of seasonal intake of nutrients contributed by the top 10 food species in the diet of *Ateles chamek* during three distinct phenological periods.

Species are sorted by percentage of total dry matter ingested. Estimated mean daily intake of nutrients and nutritional composition (%) of diets for each period is also shown.

Species	Items	%DM	%water	%ash	%CP	%AP	%TNC	%lipids	%NDF
LATE PEAK SEASON DIET: Late Wet Season (5 FAD; 24/2-6/4; 99%DM intake; 3spp excluded)									
Spondias mombin	R	45.8	36.8	44.1	55.2	29.6	47.5	38.3	36.6
Pouteria nemorosa	R (MR+R)	35.0	46.0	31.0	34.6	32.7	37.5	44.0	18.2
Ficus boliviana	I,R	5.5	3.3	10.4	15.8	10.4	1.2	5.8	21.7
Jacaratia spinosa	R	5.2	5.3	3.6	15.0	15.2	6.1	3.0	7.8
Hirtella triandra	R	3.7	3.0	3.6	4.5	2.4	3.9	3.1	3.0
Inga edulis	R	2.2	4.2	0.7	3.3	3.9	2.8	0.6	2.3
Urera baccifera	L	1.5	0.7	4.3	9.6	7.6	0.1	1.5	7.3
Syagrus sancona	F	0.5	0.4	0.7	2.7	1.1	0.3	0.6	2.1
Arboreal termite mound*	O	0.4	0.0	1.3	-	37.7*	-	2.4	-
Celtis iguanea	R	0.2	0.1	0.2	0.6	0.7	0.3	0.0	0.0
Estimated mean daily intake		273g	1971g	15g	15.6g	11.5g	151g	8.3g	34g
Between-day variation (SE)		53.3	343.5	3.4	3.6	4.5	27.8	1.6	10.0
Diet composition (% of tot dwt)				5.5	5.7	4.2	55	3.0	12
FALL-BACK DIET: Early-mid Dry Season (19 FAD; 10/4-28/6; 97% DM intake; 12 spp excluded)									
Myrciaria sp	R,I	30.5	27.2	19.2	20.4	13.5	36.2	7.2	23.9
Ficus boliviana	I,IB,R,YL	25.5	18.6	35.1	39.3	34.3	10.3	37.5	36.5
Heliocarpus americanus	YL,L	8.5	6.0	14.2	28.8	27.2	2.8	18.5	14.3
Jacaratia spinosa	L,R	8.1	11.1	4.7	13.5	21.9	16.6	6.6	4.1
Ficus trigona	R,I	7.7	19.3	8.2	7.9	5.2	5.7	8.2	7.3
Astrocarium murumuru	R	6.3	4.2	4.1	4.0	6.7	11.9	9.7	3.4
Celtis iguanea	R	4.8	4.7	4.1	7.8	15.3	11.2	0.0	0.3
Batocarpus amazonicus	LB+YL	3.2	2.8	4.2	11.0	7.8	1.1	5.4	5.2
Pseudolmedia laevis	FB	1.1	0.9	1.8	2.4	1.8	0.5	1.6	1.5
Spondias mombin	R	1.1	1.2	0.9	0.8	0.7	2.1	1.3	0.3

Cont. Appendix 3

		%DM	%water	%ash	%CP	%AP	%TNC	%lipids	%NDF
Estimated mean daily intake		248g	1309g	17g	24.1g	11.2g	76g	5.5g	96g
Between-day variation (SE)		21.0	145.4	1.6	2.4	1.4	12.7	0.7	8.9
Diet composition (% of tot dwt)				6.9	2.8	4.5	31	2.2	39
EARLY PEAK SEASON DIET: Late Dry - Early Wet Season (26 FAD; 12/7-15/9; 94% DM intake; 24 spp excluded)									
Pseudolmedia laevis	R,FB,MR,I,IB,YL	30.2	35.8	21.8	37.7	37.3	54.3	14.6	18.9
Ficus boliviana	LB,IB,R,MR,I	22.7	15.7	35.3	38.6	34.6	11.3	23.7	27.6
Myrciaria sp	R	14.5	12.0	10.3	9.8	6.8	15.8	3.8	11.3
Guazuma ulmifolia	R	8.6	2.8	4.2	7.7	6.6	6.7	3.7	13.0
Ficus trigona	R,MR,LB,I,IB,YL	8.5	20.0	10.4	9.8	7.2	5.1	8.4	9.1
Dendropanax arboreus	R	3.2	2.7	0.7	3.5	4.3	1.0	25.8	4.5
Terminalia oblonga	YL,L	2.2	1.9	4.3	6.9	7.8	0.5	3.9	3.6
Batocarpus amazonicus	LB+YL	1.7	1.5	2.7	6.0	4.4	0.6	2.5	2.9
Jacaratia spinosa	F,L	1.3	1.6	2.6	5.2	5.7	0.3	2.3	2.0
Melloa quadrivalvis	YL	1.0	0.9	1.3	5.9	11.8	0.2	1.2	1.0
Estimated mean daily intake		272g	1499g	16g	27g	12g	90g	7.3g	104g
Between-day variation (SE)		22.0	136.4	1.3	2.3	1.4	16.3	0.7	7.5
Diet composition (% of tot dwt)				5.9	9.9	4.5	33	3.2	38

In brackets after season description: FAD = number of full focal animal days included; range of dates of FAD; %of the total dry matter intake of the period represented by the listed items; number of food species recorded for the period that are not listed in this table. Column headings: Items = if multiple types of items are listed for one species, they are listed according to dominance in diet (abbreviations explained in Appendix 2); %water = proportion of fresh weight; CP = crude protein (tot N x 6.25); AP = available protein estimated from *in vitro* assay (available N x 6.25); TNC = total non-structural carbohydrates (water-soluble carbohydrates + starch); NDF = neutral detergent fiber; * Nutritional data from Dufour (1987). Protein concentration of mound likely over-estimated as the original data was analysed on termite bodies only, excluding mound material.

Photo by Annika Felton

An inspection of the observers by a subadult male spider monkey during habituation of the study community